# INSECT TRANSFORMATION

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BY

GEORGE H. CARPENTER, D.Sc.

PROFESSOR OF ZOOLOGY IN THE ROYAL COLLEGE OF SCIENCE, DUBLIN,
SECRETARY OF THE ROYAL IRISH ACADEMY

WITH 4 PLATES AND 124 OTHER ILLUSTRATIONS

METHUEN & CO. LTD.
36 ESSEX STREET W.C.
LONDON

*First Published in 1921*

TO

SIDNEY BIRKS CARPENTER

IN MEMORY AND IN HOPE

# CONTENTS

# PREFACE

SO many great names are enshrined in the literature of Insect Transformation, that the publication of a new book on the familiar theme may appear hazardous if not presumptuous. And as with lapse of time the literature accumulates, a well-balanced treatment of the subject becomes increasingly difficult. In this volume—designed to serve as an introduction to the study of growth and change in the life of insects—the author has sought, while re-telling many well-known stories, to call attention to some structural details that have hitherto escaped mention in text-books, and to discuss the relation of such details to the wider problems of insect life-histories. He ventures, therefore, to hope that the book may be of some service to serious workers in entomology as well as to beginners.

Descriptions of the form of adult insects are given only in so far as is necessary to elucidate the structure of larvae, pupae, and immature stages generally. No attempt has been made to compile a bibliography, but references are given to books and papers to which the writer is indebted, and full lists of titles are to be found in many of these. Especial acknowledgment is due to the writings of A. S. Packard, L. C. Miall, L. F. Henneguy, J. H. Comstock and R. J. Tillyard.

The source of every borrowed illustration is indicated in its title, and the thanks of the author and publishers are rendered to the United States Department of Agriculture, the Cambridge University Press, and the Royal Dublin Society, for the loan of blocks. The Cambridge Press has generously allowed the use of several figures from the author's "Life-story of Insects," and from Dr. Tillyard's "Biology of Dragon-flies," while Prof. J. H. Comstock has kindly granted the use of illustrations from "The Wings of Insects," and from his lately-published "Introduction to Entomology."

The author is indebted to Miss Eileen E. Barnes for the care and skill wherewith she has re-drawn many of the figures. He would also gratefully acknowledge valuable aid in proof-revision from his colleagues, J. N. Halbert of the National Museum, and D. S. Torrens of the Royal College of Science, Dublin. The last-named has added the labour of index-making to many acts of kindly help.

G. H. C.

DUBLIN, *August*, 1921

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## CHAPTER I

## INTRODUCTION

AN observant rambler in field or woodland on a summer day cannot fail to be struck by the variety and abundance of the insect life around him. Grasshoppers chirp in the herbage at his feet, dragon-flies pursuing their prey swoop in rapid flight through the air; butterflies flit and bees linger about the flowers; while the rambler himself serves as a centre of attraction to hundreds of small flies, some of which probably try to feed on his blood. He need evince no surprise should he be told that the number of different kinds of insects exceeds by far that of all other groups of animals taken together; and if natural objects have any hold upon his thought, he can hardly fail to realize that the Insect World may furnish abundant material for studies of absorbing interest.

Probably he knows that the hosts of delicately-formed winged creatures around him, have passed through a wonderful process of growth and change in the course of their short lives. At least he is well aware that the gaily-coloured butterfly, unable to bite and feeding on the nectar of blossoms, has developed from a crawling caterpillar which masticated leaves and devoured them in solid pieces. The honey-bee that also haunts the blossoms was once a soft grub, lying helpless and dependent in a waxen chamber of the comb. The flies that buzz around the intruder have come from a childhood passed as grubs or maggots in a vast variety of sheltered situations

where food was plentiful, such as the inside of plant-tissues, the carcase or excrement of some animal, the mud of the pond-shore, the waters of the ditch or stream. The dragon-fly's few weeks of aerial hunting are preceded by a year or two of lurking existence as a crawling " larva " or " nymph " at the bottom of the pond or river. Growth accompanied by change is thus the rule of life in the insect world.

Somewhat more detailed study shows us that the changes which accompany growth vary greatly in their extent in different groups of insects. Let us start, for example, with the transformation that is more familiar than any other—that of the caterpillar into the butterfly. There are many striking features of difference: the caterpillar is wingless, crawling, biting; the butterfly is winged, flying, sucking. Yet in both there are obvious correspondences, such as the firm head capsule with its feelers, and behind the head the three segments of the fore-body, each segment with its pair of legs. A greater difference than this is noticeable between the wasp or bee and its grub; though the latter has a head-capsule distantly resembling that of its parent, it has no legs of any kind. And between the blow-fly and its maggot, there is a divergence still greater, for the maggot is not only without legs, but without a recognizable head-region. Thus the life-stories of a butterfly, a bee, and a blow-fly form a series illustrating increasing divergence between the larva (as all young creatures unlike their parents are commonly called) and the imago (or adult, winged creature). In all these insects there is much change during growth, and the greater the difference between larva and imago, the more profound the change must be. Between the larva and the imago comes, in the course of the life-history, the resting stage which is called the " pupa " or " chrysalis "; before and during this period much reconstruction of the body necessarily takes place. It is noteworthy that in butterfly, bee, and blow-fly, no trace of wings can be seen until the pupal condition has been assumed.

If, however, the life-story of a dragon-fly be compared with that of a butterfly, considerably less distinction between the young and the adult insect is to be noticed. There are indeed striking differences in many details of structure, notably in the jaws, and the immature insect living under water has

special provisions enabling it to breathe dissolved air. But in its general build—its broad head, its six conspicuous legs, its tapering hind-body—the aquatic larva of the dragon-fly resembles its parent far more closely than the caterpillar resembles the butterfly. And, in marked contrast to the course of growth in the life of the last-named insect, the young dragon-fly at an early age possesses on the second and third segments of the fore-body visible rudiments of wings, which become larger as the creature passes from stage to stage of its existence.

Further, if the observer can find specimens as young as possible of the insect first mentioned in this brief survey, a grasshopper, he will see at once that the little creature resembles its parent as unmistakably as a kitten resembles a cat, or a cygnet a swan. The baby grasshopper has the same general shape of body as the adult, the same long, strong hind-legs serviceable for jumping ; it lives in the same situation as its parent and devours the same kind of food. As yet, indeed, it has no trace of wings ; but early in the course of its growth rudiments of these organs appear on the proper body-segments, and they become more prominent at each successive stage.

Lastly, should our rambler turn over a stone or pull a strip of bark from a dead tree-trunk, he will probably see a number of tiny insects actively leaping about. They are spring-tails, and if they be examined with a lens it will be found that the young closely resemble the adults, which differ from all the fully-grown insects mentioned hitherto, in having no wings. In the case of these spring-tails, therefore, there is even less difference between the young and the adult than in the case of the grasshopper, as in all its stages a spring-tail is wingless.

These few examples are sufficient to illustrate superficially the varying degrees of change among insects during their growth from the newly-hatched young to the perfectly-formed adult. A wide field of inquiry is thus opened up, and it will be found that a study in some detail of the stages through which these and similar creatures pass will afford facts of surpassing interest and suggest lines for fascinating speculation. Before entering more fully, however, on the

subject of these life-histories, an introductory account of the form and nature of a typical insect must be given. It will then be realized how the very foundation-plan of the creature's body is necessarily linked with the changes through which it has to pass during its time of growth.

## CHAPTER II

# FORM, GROWTH, AND CHANGE

IT may seem paradoxical to begin the study of development among insects with the examination of a fully-grown specimen of the group, but it is towards this adult condition that development tends. The caterpillar may be regarded from one view-point at least, as the preparation for the butterfly ; and the structure and habits of the immature creature can be satisfactorily explained only in the light of what is to be the end of its life-story.

It is common knowledge that in most groups of animals, the naturalist can distinguish more or less easily between "lower" or more generalized and "higher" or more specialized members. The organs of a creature of the latter grade can be understood only by comparing them with the corresponding parts in a more lowly relation, and it is now generally believed that specialization of any kind of living creatures has been attained by progressive changes from simple beginnings, not only in the life-story of the individual but also in the history of the race. Therefore, in a study of insect structure, it is inadvisable to begin with so highly organized and specialized a creature as a butterfly, a bee, or a blue-bottle. Some more simply-built insect will be more suitable, though we may indeed find that the most simple furnish us with details sufficient for years of research. We can profitably start with an insect like that first mentioned on the first page of this book—a grasshopper or locust (Fig. 1)—which belongs to a comparatively lowly order, and shows, as already mentioned, no striking difference between the young and the adult.

The outer covering of the body is for the most part hard and firm ; it may fairly be described as horny. Such a firm cuticle characterises generally all members of the *Arthropoda*, a great

group or Phylum[1] of the animal kingdom to which not insects only, but also shrimps and crabs, spiders and scorpions, centipedes and millipedes belong. This cuticle is not a hardened skin, consisting of transformed cells, once living units of the

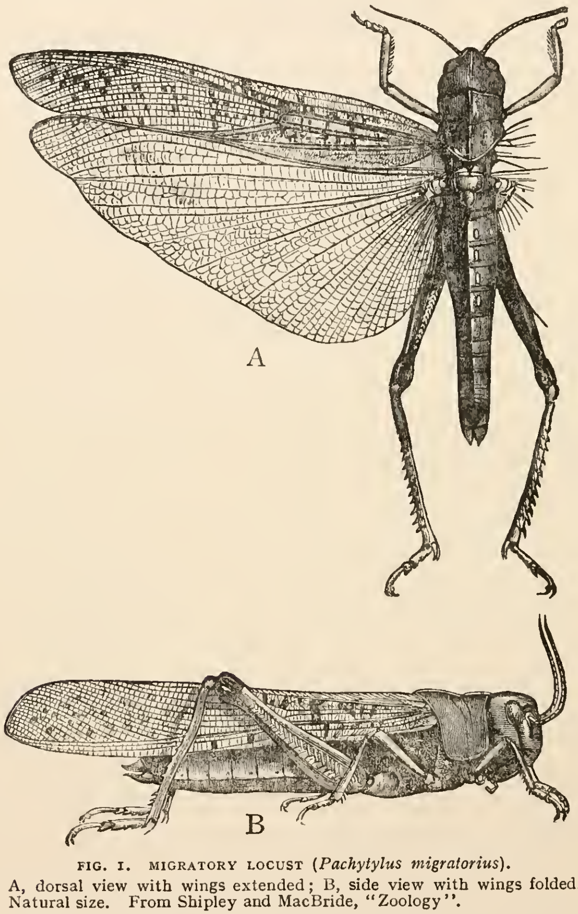



FIG. I. MIGRATORY LOCUST (*Pachytylus migratorius*).
A, dorsal view with wings extended; B, side view with wings folded. Natural size. From Shipley and MacBride, "Zoology".

creature's growing tissue. It is a lifeless envelope built up (or *secreted*) by the skin which remains as a living sheet of cells beneath it; its chief constituent is a horny substance known as *chitin* (Fig. 2). Being a secreted cuticle and not a living skin

[1] Indicating a race of creatures believed to be linked together by community of descent.

(or *epidermis*[1]) it cannot grow, and there are limits beyond which it cannot be stretched. From this it follows that an insect or other arthropod must needs shed its cuticle periodically during its growth, a new cuticle, at first thin and delicate, being formed beneath the old one, to be revealed after the " moult " (or *ecdysis*) is over. Where, as is often the case, successive layers of the cuticle can be distinguished, the older (primary) layer (Fig. 2 $cu_1$) is at the surface, the newer layers ($cu_2$) deeper next the skin. The cuticular nature of the insect's outer envelope (or *exoskeleton*) and the consequent necessity for its periodic renewal and casting, are most important factors in determining the course of insect transformations.

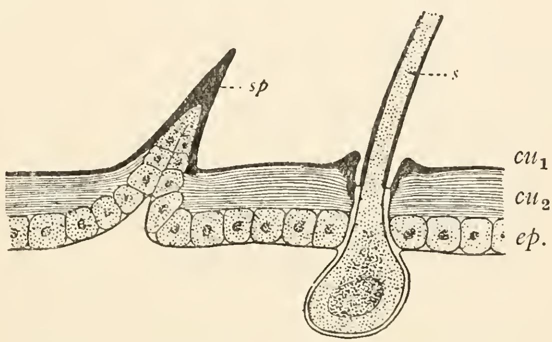



FIG. 2. SECTION THROUGH THE SKIN (*ep*) AND CUTICLE (*cu*) OF AN INSECT.

$cu_1$, primary, and $cu_2$, secondary cuticle ; *sp*, a rigid spine : *s*, a flexible " bristle " or " hair " ; somewhat diagrammatic and highly magnified. From Comstock, " Introduction to Entomology ".

Closer study of the cuticle of our grasshopper shows that it is not uniformly thick and firm ; were it so the whole exoskeleton would be rigid, whereas there are many parts that can be readily moved in relation to each other. If we examine the hind-body (or *abdomen*) of the insect, we see that the cuticle may be roughly described as consisting of a series of firm skeletal pieces (or *sclerites*) connected by short regions of thin and flexible membrane. These sclerites of the exoskeleton indicate the *segments* of which the abdomen is built up, and in arthropods generally the body is segmented, the segmentation being

[1] Most writers on the structure of insects use the term *hypodermis* for this cell-layer.

usually well marked in the divisions of the cuticle. Examining one of the legs, we notice that here again are long tubular pieces of hard chitin, such, for example, as the "thigh" and the "shin," while between them, as at the "knee" joint, are flexible regions, so that the leg can be bent or straightened by means of the contraction of its internally-placed muscles. In these jointed legs (Fig. 6) of an insect we see another character which it shares with a lobster or a spider, a character common to arthropods generally, and indeed giving the name —Arthropoda (or "Joint-footed")—to the whole group. The exoskeleton is evidently the feature of an insect to which the student of structure must naturally turn first, for its form and arrangement determine the outward appearance of the creature, and it serves as a general framework for the internal organs of the body.

Reference has already been made to the segmentation—the repetition of similar parts from before backwards—which is a marked characteristic of all arthropods. In the body of a grasshopper (Fig. 1) it can readily be seen that the segments are grouped in three regions. Foremost is the *head* carrying a pair of eyes, a pair of feelers, and three pairs of jaws; the general rule among arthropods is for a segment to bear one pair of limbs or appendages and no more, we conclude therefore that there must be at least four segments in this insect's head. Next comes the *thorax* (or fore-body), which has three segments, each carrying a pair of *legs*—six legs being the usual number for any insect; further, the second and third segments of the thorax carry each a pair of *wings*. Bearing as it does, legs for walking and wings for flight, this region is evidently the centre of the creature's locomotor activities. Behind is the long *abdomen* (or hind-body) in which ten distinct segments can be recognized, most of these are evidently limbless, but appendages or outgrowths concerned with the functions of egg-laying can be seen towards the female's extreme hinder end, and the tenth segment carries a pair of short limbs—the "tail-feelers" (or *cerci*).

It is now necessary that the structure of these regions of the body should be studied in some detail.[1] The exoskeleton of

[1] A. S. Packard: "A Text-book of Entomology". New York, 1898. L. F. Henneguy: "Les Insectes". Paris, 1904. A. Berlese: "Gli Insetti", Milano, 1909.

the head consists of a number of sclerites firmly joined together, so as to build up a firm, hollow capsule. On top is the crown (or *epicranium*, Fig. 9 *ep*), in front, the forehead (or *frons*) above, and below the face (or *clypeus*), to which is hinged the upper lip (or *labrum*, Fig. 9 *la*), bounding the mouth in front; at the sides are the cheeks (or *genae*, *ge*), and the conspicuous oval *eyes*.

Examined with a strong magnifier the surface of each eye is seen to be made up of hundreds of six-sided areas, resembling the cells of a honey-comb; these are the corneal facets, each of which has beneath it a series of nervous structures, forming an element (or *ommatidium*) of a compound eye. Compound eyes, closely similar to those of most insects, are found in shrimps, crabs and other members of the Crustacea; such creatures have their compound eyes at the tip of stalks which may be regarded as shortened limbs. Therefore it is possible that these organs really represent a pair of appendages; from the manner in which they develop in the embryo before hatching, we know that they belong to a head-segment situated in front of the one that bears the feelers.

The feelers (or *antennae*) are elongate, jointed appendages which, when examined with a strong lens are seen to be clothed somewhat densely with structures that may be described as fine "hairs" resembling as they do in appearance the hairs of the human head for example. But while the hairs of a back-boned creature are modified parts of the skin, the "hairs" or "bristles" of an insect or a spider are modified parts of the cuticle, each hair jointed on to the surrounding area by a piece of flexible membrane (see Fig. 2, *s*). An insect hair or similar structure has been formed by a special cell of the underlying skin; if this cell be continued as a nerve-fibre leading to the central nervous system, the hair is "sensory" in function, so called because through it the cell in the skin can be stimulated so as to transmit a nerve-impulse inwards, which may be presumed to give rise to something in the insect's consciousness resembling sensation in our own. The hairs on an insect's feeler are to a large extent sensory, some being regarded as concerned with touch and others with a sense akin to smell.

Very different from the slender, flexible feelers are the strong

biting *mandibles* (Fig. 3 *Mnd*) the foremost of the three pairs of limbs associated with the grasshopper's mouth and modified as jaws. The mandible is a stout, hollow, sub-conical piece of chitin with sharp teeth near the apex and a ridged grinding area near the base on the inner face, so arranged as to work with the corresponding structures on the opposite mandible, and thus to cut and grind the insect's food. The mandibles

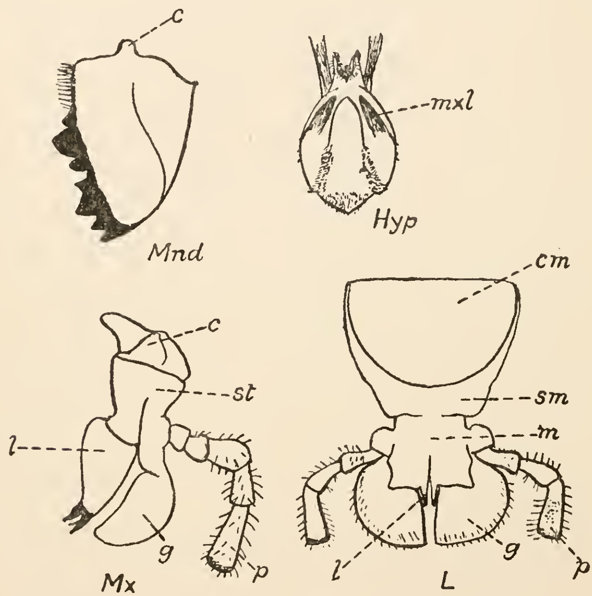



FIG. 3. JAWS OF A WEST AFRICAN LOCUST (*Rutidoderes*). *Mnd*, mandible; *c*, condyle. *Hyp*, tongue with maxillulae (*mxl*). *Mx*, maxilla; *c*, cardo; *st*, stipes; *l*, lacinia; *g*, galea; *p*, palp. *L*, labium; *cm*, cuticle of neck; *sm*, sub-mentum; *m*, mentum; *l*, lacinia; *g*, galea; *p*, palp. × 6.

articulate with the head skeleton so that they can be made to clash together through the action of *adductor*, or can be drawn apart through the action of *abductor* muscles.

Behind the mandibles are situated the *maxillae* (Fig. 3 *Mx*), a pair of limbs at once more delicate and more complex than the mandibles, though, like those, modified to assist in feeding. In the grasshopper each maxilla has a three-segmented base formed of two larger sclerites, the *cardo* and the *stipes* (Fig. 3,

*c*, *st*), with a smaller one at their junction; the stipes bears a sharp inner and a blunt outer lobe (called respectively the blade or *lacinia* and the hood or *galea*) and a leg-like jointed *palp* (Fig. 3, *l*, *g*, *p*). The mouth is bounded behind by a pair of appendages in which parts corresponding to those of the maxillae can readily be recognized, but which are joined together by their bases so as to form a *labium* (Fig. 3 *L*) or "lower lip." As this structure is, in grasshoppers and some related insects, evidently connected with the cuticle of the flexible neck-region between the head and thorax it may probably be regarded as belonging to the segment immediately behind the head rather than to the head itself, with which, however, it is closely knit in beetles and in most other insects.

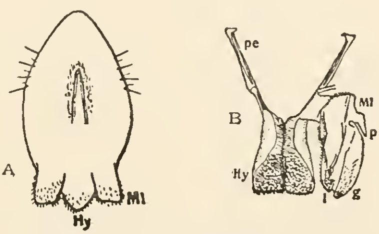



FIG. 4. HYPOPHARYNX OR TONGUE (*Hy*) AND MAXILLULAE (*Ml*) OF EARWIG (*Forficula*, A), AND BRISTLE-TAIL (*Petrobius*, B). In the latter, lacinia (*l*), galea (*g*), and palp (*p*) are recognizable. × 20.

The eyes, feelers, mandibles, maxillae and labium are recognizable in the great majority of insects, and from their presence we infer that at least five segments enter into the composition of the head. Deeper study of the subject suggests the probability that other segments may, in some cases, be represented. In the centre of the grasshopper's mouth there is a blunt tongue (or *hypopharynx*) (Fig. 3 *Hyp*) with cuticle partly membranous and partly firm, bearing a number of fine hairs; on the front face of this tongue a pair of narrow, elongate sclerites (*mxl*) can be clearly seen. If, now, the tongue of an earwig be examined for comparison it will be found that in a position corresponding to that of the sclerites just mentioned, a pair of prominent rounded lobes are attached by their bases to the tongue and project beyond it (Fig. 4 A). In a similar situation in the mouth of some of the wingless spring-tails and bristle-tails,

these lobes are so strongly developed (Fig. 4 B) as to suggest that they represent a pair of jaws—known as the *maxillulae*—lying between the mandibles and the maxillae. Further it has been shown that, in some insects, the embryo, as it develops in the egg, has a segment with a pair of rudimentary limbs between the feelers and the mandibles. Thus the conclusion is reached that the insectan head may contain not five segments only, but seven[1] including that to which the labium belongs. Such studies are of interest, because they throw light on the history of structures which undergo progressive changes during the evolution of the race. It seems that the compact head of a grasshopper or a beetle has arisen from the association of seven segments, originally distinct, each one bearing its pair of appendages ; of these seven, the third and fifth have now become so reduced as to be hardly recognizable, while the seventh was, so to say, annexed by the head after the others had been incorporated into the primitive head-skeleton. The composition of the insectan head has been explained with some detail because the parts are often strangely modified during the early stages of an insect's life.

By means of a flexible neck—probably representing the segment of the labium—the grasshopper's head is joined to the great central region of the body, the *thorax*. This is composed of three segments known respectively as the *prothorax*, *mesothorax*, and *metathorax*, and in each segment may be distinguished various sclerites which build up the *tergal* surface above, the *sternal* surface beneath, and the *pleural* areas at the sides. The tergal sclerite of the prothorax is extensive, a firm hood-shaped plate distinguished as the *pronotum* (Fig. 9 *pr.*) which reaches backwards so as partly to overhang the segments behind. In each of these a series of sclerites, whose boundaries are marked by grooves in the cuticle, may be distinguished—from before backwards these are defined as *prescutum*, *scutum*, *scutellum*, and *post-scutellum* (Fig. 5 *Psc*, *Sct*, *Scl*, *Pscl*). We notice that the scutellum is subtriangular in shape, the apex directed backwards ; in some insects the mesothoracic scutellum is relatively much larger and more conspicu-

[1] J. H. Comstock : " An Introduction to Entomology". Ithaca, New York, 1920. J. H. Comstock and C. Kochi : "The Skeleton of the Head of Insects". *Amer. Nat.*, XXXVI. 1902. J. W. Folsom : " Entomology". Philadelphia and London, 1906.

ous than in the grasshopper. In the sternal or lower (ventral) area of a thoracic segment, the bilobed central *sternum* (Fig. 5 *S*) is the most prominent sclerite, behind this is a *post-sternum* (Fig. 5 *Psl*) and on either side, extending to the insertion of the leg an *episternum* (Fig. 5 *Eps*) this latter together with an *epimeron* (Fig. 5 *Epm*) lying behind it, reaches upwards to the base of the wing in the mesothorax and metathorax, forming the pleural area of the exoskeleton.

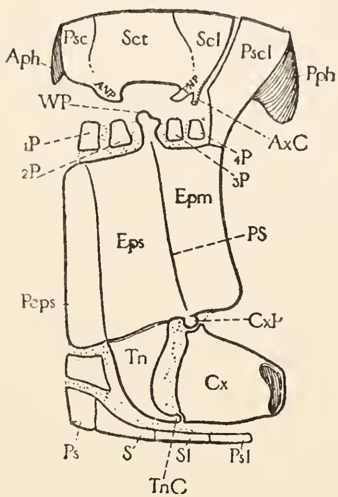



FIG. 5. DIAGRAM OF INSECTAN MESOTHORAX (side view). *Psc*, prescutum; *Sct*, scutum; *Scl*, scutellum; *Pscl*, post-scutellum; *Aph*, *Pph*, phragmata for muscle attachment; *Anp*, *Pnp*, notal wing processes; *WP*, pleural wing process; 1, 2, 3, 4 *P*, basal wing-sclerites; *Peps*, pre-episternum; *Eps*, episternum; *Epm*, epimeron; *Ps*, pleural suture; *CxP*, coxal process; *Cx*, coxa (haunch) of leg; *Tn*, trochanteria; *Tnc*, its coxal articulation; *Ps*, presternum; *S*, sternum; *Sl*, sternellum; *Psl*, poststernum. After Snodgrass, *U.S. Dept. Agric. Entom. Tech. Ser.* XVIII.

Each segment of the thorax carries a pair of *legs*, the leg being inserted on either side between the sternal and pleural regions. The leg (Fig. 6 A) is a beautifully jointed organ built up of a series of sclerites united by short tracts of flexible cuticle. The basal segment is a stout haunch (*coxa*) linked by a small *trochanter* to the long thigh (*femur*), to which at the knee-joint is attached the spiny shin (*tibia*); at the far end of this comes the foot (*tarsus*), which in the grasshopper is

built up of three segments, the terminal one carrying a pair of strong claws and a central pad or *pulvillus*. The number of foot-segments varies in different insects; in most adult insects there are five (Fig. 6 B), and where fewer are present, it is believed that diminution from the primitive number has taken place. This is indeed quite evident in some cases, where the apparently absent segments may be recognized in a reduced condition.

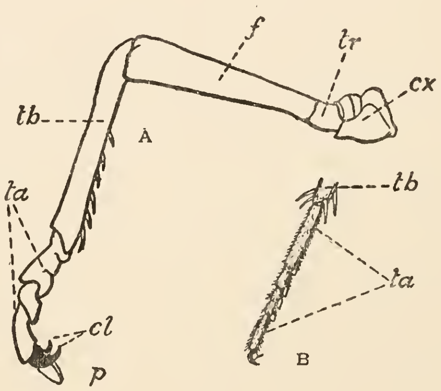



FIG. 6.

A, Intermediate leg of a locust (*Rutidoderes*). *cx*, haunch; *tr*, trochanter; *f*, thigh; *tb*, shin; *ta*, foot; *cl*, claws; *p*, pulvillus. B, tip of shin (*tb*) and five segmented foot (*ta*) of cockroach (*Periplaneta*). × 2½.

While many insects have the legs of the three pairs closely alike, grasshoppers and their allies are remarkable for the excessive size of the hindermost legs, in which both thigh and shin are greatly lengthened relatively to those of the other two pairs, the thigh being strong and stout at the base, tapering gradually towards the tip. This modification confers on these insects their well-known power of leaping. The grasshopper's leap results from the sudden straightening or extension of the hind legs; when the insect is at rest these limbs are sharply bent or flexed at the knee-joint (Fig. 1). The straightening or the bending of the leg is caused by the contraction of alternative sets of muscles known respectively as the *extensors* and the *flexors*. The large size of the grass-

hopper's hind thigh is necessary for the inclusion and attachment of the great muscles which move the shin.

The structure of the legs is of importance to the student of insect transformations because these organs show varying degrees of development in different insect-larvae both as compared with one another and with the perfect insects into which they grow.

The second and third thoracic segments—mesothorax and metathorax—are outstanding because to them are attached the *wings*, those characteristic organs for effecting the insect's motion through the air. An insect's wing[1] must be regarded as a lateral outgrowth of the body, bounded by a thin extension of skin covered outwardly by cuticle, the whole structure flattened from above downwards so that the original cavity becomes to a great extent obliterated, and the wing appears to be a sheet of membrane, more or less rigid, jointed at the base between the tergal and pleural regions of the segment that bears it, where the powerful muscles which either lower or raise the wing (*depressors* and *elevators*) find their attachment. The surface of the wing does not present a uniform aspect; it is traversed by series of tube-like supporting structures variously known as "nerves," "veins" or "ribs", but for which the term *nervures* is preferable..

In the grasshopper we notice that the two wings on the same side (Fig. 1 A) differ markedly from each other. The *forewing* (Fig. 7), carried on the mesothorax, is of firm texture, rigid and brittle, elongate and narrow, with almost straight edges and a rounded tip. The *hindwing* on the metathorax, is more delicate, and may be described as subtriangular with the corners rounded; when extended from the body, its front margin is fairly straight and the area of the wing next this is more rigid than that region which, lying behind and nearer to the abdomen, can be folded fanwise beneath the firmer forward area. When the wings, not in use for flight, are laid back over and alongside the body (Fig. 1 B), the forewings completely hide and protect the comparatively delicate hindwings, that are partly folded beneath them. In the grasshoppers and their near allies the wings of both pairs are serviceable for flight, though the forewings are, as we have

[1] J. H. Comstock: "The Wings of Insects". Ithaca, New York, 1918.

seen, to a great extent protective. With such an arrangement may be contrasted, on the one hand, that found in dragonflies, where fore- and hindwings are alike flying-planes of great strength and rigidity, and on the other hand, the highly-specialized condition in many beetles, where the forewings are modified into hard, thickened sheaths, the hindwings alone being used for the support of the insect when flying.

As the changes through which insects pass during their lives are largely concerned with the development of the wings, the form and arrangement of these organs are worthy of attention in some detail. The wing is attached at its *base* to the segment that bears it, articulating with the exoskeleton of the thorax by means of a group of firm sclerites (Fig. 5, 1, 2, 3, 4 *P*) the outermost of which are continuous with the principal longi-

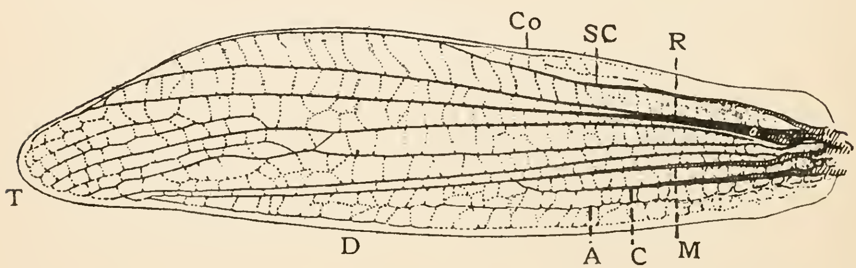



FIG. 7. FORE-WING OF MALE GRASSHOPPER (*Stenobothrus*).
*Co*, costa; T, termen; *D*, dorsum; *SC*, subcostal; *R*, radial; *M*, median; *C*, cubital; *A*, anal nervures. × 8. From Comstock, "Introduction to Entomology".

tudinal nervures described below. The front edge of the wing, when extended at right angles to the axis of the body is called the *costa* (Fig. 7 *Co*), the hinder edge the *dorsum* and the outer boundary the *termen*. In the large sub-triangular hindwing of the grasshopper the dorsum and termen are both extensive, but in the narrow forewing with its rounded tip these sections of the margin are hardly distinguishable except as indicated by the nervuration. The longitudinal nervures which traverse the wing from base to termen are of great functional importance because they are the chief support of the delicate wing-membrane; they are also valuable guides to the student of insect classification and development. Running nearly parallel to the costa is the *sub-costal* nervure, then connected with the same group of basal sclerites, the great *radial* trunk which

gives off the branched *radial sector.* Close alongside the radial is the *median,* though this springs in some cases from the hinder group of sclerites, associated in its origin with the *cubital* and *anal* nervures, the last-named two or three in number. The area traversed by these anal nervures in the hindwing is that which can be folded fanwise beneath the firmer front region, and in many insects a similar arrangement is to be noticed.

The radial, median and cubital nervures are often branched to a greater extent than in the grasshopper, five radial, three

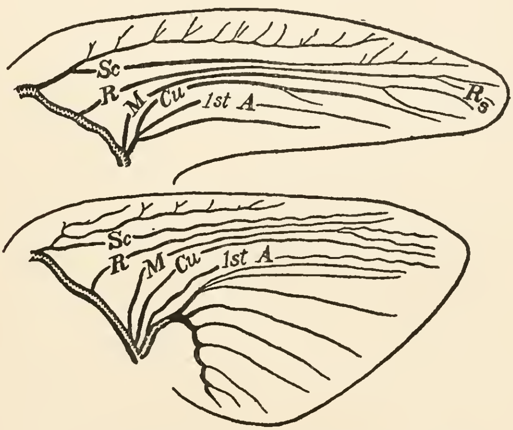



FIG. 8. WING-RUDIMENTS OF AN IMMATURE GRASSHOPPER, SHOWING TRACHEAL TRUNKS.

*Sc,* sub-costal; *R,* radial (*Rs,* radial sector); *M,* median; *Cu,* cubital; 1st *A,* first anal. After Comstock, "Wings of Insects".

or four median and two cubital branches being frequently recognizable (Figs. 35, 87). Between the longitudinal nervures fine transverse nervules are often developed in large numbers, and this condition is strongly marked in the grasshopper, whose wing-areas present the appearance of a complex network. The larger nervures contain blood-spaces and are traversed by air-tubes, outgrowths of the remarkable breathing-system of the insect that has yet to be considered. The growth of these air-tubes or tracheal trunks into the cavity of the developing wing indicates the general course of the subsequently formed nervures (Fig. 8).

Behind the thorax with its legs and wings, extends the elongate *abdomen* or hind-body of the grasshopper. In this region ten segments may be readily distinguished, most of them simple in construction, destitute of limbs, and closely similar to one another, the exoskeleton consisting of a strongly-arched tergum above and a flattened sternum beneath. On either side of the first abdominal segment is a specialized, thin, tense, circular area of cuticle—the *tympanum* or drum of an organ of hearing (Fig. 9 *t*). The sternum of this segment is imperfectly developed on account of the backward extension of the thoracic metasternum while the tenth segment carries a pair of short but definite limbs, the *cerci* or tail-feelers (Fig. 9 *c*). Behind this, small dorsal and ventral sclerites surround the

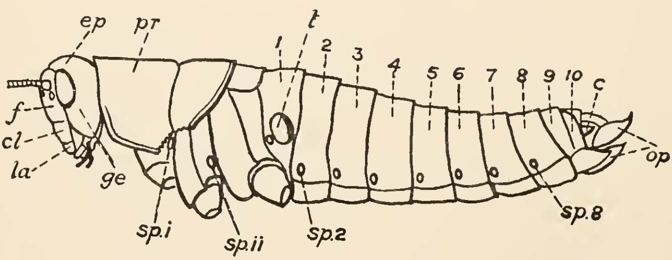



FIG. 9. SIDE-VIEW OF A LOCUST WITH WINGS AND LEGS REMOVED.
*ep*, crown; *f*, frons; *cl*, clypeus; *la*, labrum; *ge*, cheek; *pr*, pronotum; 1–10 abdominal terga; *sp.i*, *ii*, thoracic spiracles (the first exposed by removal of corner of pronotum); *t*, ear-drum; *sp.*2, 8, second and eighth abdominal spiracles; *c*, cercus; *op*, ovipositor. Natural size.

vent or intestinal anus; these may be regarded as the exoskeleton of a terminal tail-segment. In the female grasshopper there are three pairs of hard processes, one pair belonging to the eighth and two pairs to the ninth abdominal segment; these form the egg-laying organ or *ovipositor*, and their strong, sharp tips extend backwards beyond the rest of the abdomen (Fig. 9 *op*).

Close examination of the grasshopper's exoskeleton reveals the presence of a series of paired openings (Fig. 9 *sp*) on the sides of many of the segments. These are the *spiracles* or *stigmata*, by means of which the insect's breathing organs are in connexion with the atmosphere. The foremost of them are seen on the thin cuticle between the pronotum and the meso-

thoracic pleura ; the second pair may be found on the similar delicate connexion between the mesothorax and the metathorax close to the bases of the intermediate legs. Thus there are two pairs of spiracles (Fig. 9 *sp.* i, ii) on the thorax. The abdomen carries eight pairs of these openings, situated on the successive segments from the first to the eighth inclusive ; each spiracle is close to the lower margin of the tergum and towards the front edge of the segment (Fig. 9 *sp.* 2, 8).

The system of *air-tubes* (or *tracheal* system) to which these spiracles lead is among the most wonderful and characteristic features of an insect's body (Fig. 10). An air-tube has a delicate cellular wall (Fig. 11 *ep*), lined with what is really an extension of the outer cuticle, thickened spirally (Fig. 11 *ct*) so as to strengthen the tube and prevent it from collapsing. The tubes branch repeatedly and their fine endings (*tracheoles*) are distributed (Fig. 11 *tl*) so as to be in close contact with the various tissues.

Two main trunks extend lengthwise, one along either side of the insect, connected with the successive spiracles by short lateral tubes, and giving off branches ventralwards and dorsalwards ; the latter series lead into paired longitudinal dorsal trunks which run one on either side of the tubular heart ; they are also connected with large bladder-like air-sacs (Fig. 10 *a. s*) arranged segmentally in pairs. The branches of the main longitudinal trunks fork repeatedly, and finally give rise to the minute thin-walled tubes or tracheoles (Fig. 11 *tl*) through which the living tissues of the insect obtain the oxygen necessary to support the combustion-process constantly going on, and give up the carbon dioxide which passes with the expired air out of the spiracles.

To the student of anatomy, the most striking feature about the air-tubes of an insect is that they are lined with an extension of the creature's chitinous outer cuticle. The cellular walls (Fig. 11 *ep*) of the air-tubes, which make the chitinous lining must be regarded therefore as inpushings of the skin, and this view is confirmed, not only by the origin of the tracheal system in development, but also by the fact that at each moult the chitinous linings of the air-tubes are cast off with the exoskeleton and re-made.

It has been mentioned how the longitudinal air-tubes of

the upper pair run on either side of the long tubular *heart* (Fig. 10 *h*). This important organ extends in insects along the central axis of the body just below the dorsal wall, lying in a shallow chamber (*pericardial blood-space*) (Fig. 10 *pc*) bounded above by that wall and beneath by a delicate, perforated mem-

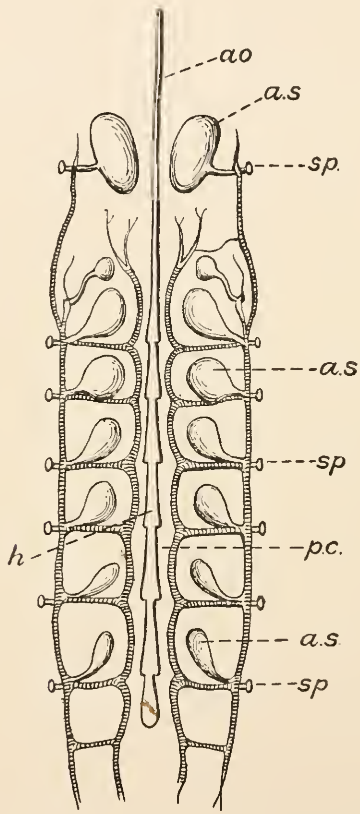



FIG. 10. DIAGRAM OF HEART (*h*) AND PART OF AIR-TUBE (TRACHEAL) SYSTEM OF A LOCUST.

*ao*, aorta; *pc*, pericardial space; *sp*, spiracles; *as*, air-sacs. ×2. In part after Emerton (Packard's "Text-book.")

brane which roofs in the main cavity of the body. After being propelled along the heart, by rhythmic contraction of its muscular wall, from behind forwards, and then through tubular vessels (*arteries*), the blood passes into this main cavity. This arrangement of the blood-system affords a marked contrast

to that usual in most animals, whose blood circulates through a continuous system of closed vessels. In insects the nutrient and cleansing fluid escapes from the vessels into great blood-spaces, so as to bathe the various organs, and of these spaces the main body-cavity is the largest. Thence the blood passes upwards, through the perforations in the delicate roof, into the pericardial blood-space, and re-enters the heart through a series of paired slits, guarded by valves, in the wall of that organ.

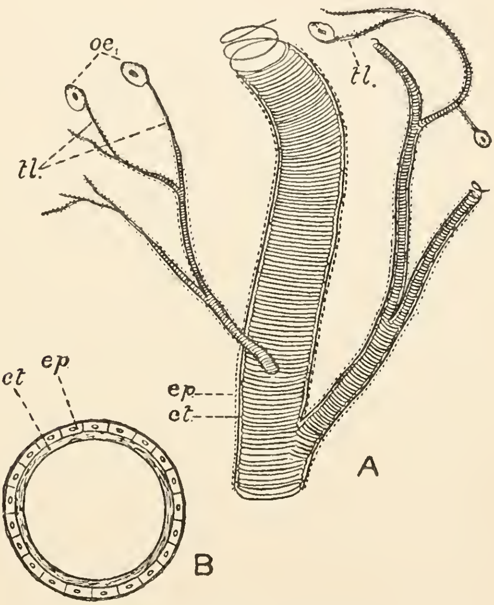



FIG. II. AIR-TUBES IN SURFACE VIEW (A) AND IN CROSS-SECTION (B). DIAGRAMMATIC.
*ep*, cell-layer or epithelium ; *ct*, cuticular lining ; *tl*, tracheoles ; *oe*, oenocytes. (A) × 30 ; (B) × 100.

This last-mentioned arrangement of openings which allow blood to pass inwards through the wall of the heart, is one of the most remarkable of the characters that distinguish not insects only but the whole great group of arthropods from all other animals. It is impossible, in this book, to deal adequately with physiological questions, but it may be pointed out here that the living tissues of an insect are everywhere directly bathed by the blood and are directly in

touch with the outer air through the tracheal tubes ; hence it may be realized that the insect's body is admirably adapted for those rapid transformations of energy which are necessary for its vigorous life-activities.

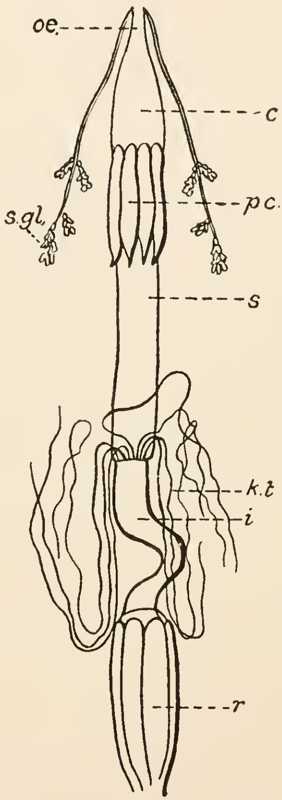



FIG. 12. DIGESTIVE SYSTEM OF LOCUST.
*oe*, gullet ; *c*, crop ; *sgl*, salivary glands ; *s*, stomach ; *i*, intestine ; *kt*, kidney or Malpighian tubes ; *r*, rectum. Slightly magnified and somewhat diagrammatic. In part after Emerton and Burmeister.

In the great blood-cavity below the pericardial space, the most prominent objects are the *organs of digestion* (Fig. 12). The mouth, surrounded, as we have seen, with jaws for the mastication of the food, leads into a narrow *gullet* (or *oesophagus*) which widens into the large pear-shaped *crop* (Fig. 12 *c*) that may extend backwards into the abdomen. Along-

side the crop are situated the paired *salivary glands* (*s gl*), the fluid secreted by which passes through a set of fine tubes or *ducts* into a median duct that opens into the mouth behind the base of the tongue. The gullet and crop are—like the air-tubes—lined with an extension of the cuticle ; so is the small *gizzard* (or *proventriculus*) lying immediately behind the crop ; the chitinous lining of the gizzard is thickened into teeth and ridges and beset with hairs, so that this organ serves for crushing, pressing and straining the food. Next comes the tubular *stomach* (or *ventriculus*) which has no chitinous lining, its inner or mucous coat consisting of a sheet of glandular and absorbent cells. This region (Fig. 12 *s*) is often known as the *mid-gut.* Just behind the gizzard, the stomach gives off a series of blind tubes (Fig. 12 *pc*) within which digestive juices containing ferments that act on the food substances are formed, and whence they are poured into the food-canal. Behind the stomach is seen a narrower tube the *intestine* (Fig. 12 *i*) which again has a chitinous lining, as has the somewhat swollen terminal region of the digestive tube known as the *rectum* (Fig. 12 *r*), whence the waste residue of the food-stuffs is passed out of the body through the vent or *anus.*

A remarkable feature of the insect's food-canal is that at either end an extensive region is lined with a continuation of the outer cuticle—the gullet, crop and gizzard in front, and the intestine and rectum behind. These two regions are known as the *fore-gut* and the *hind-gut* respectively, and their living linings—the sheets of cells on whose inner surface the cuticle is formed—must be regarded as inpushings of the skin. The cuticular lining of these regions is shed at each moult along with the exoskeleton. The digestive system is therefore directly concerned in the changes that accompany growth, and in those cases where the adult insect has a manner of feeding differing widely from that of the young, these changes may be necessarily very great.

At the junction of the hind-gut with the mid-gut a number of fine tubes with cellular walls are given off so as to float freely in the great blood-space. These (Fig. 12 *k t*) are usually called *Malpighian tubes,* being named after the eminent Italian anatomist of the seventeenth century, Marcello Malpighi, who made monumental studies on the minute structure of insects. They

might appropriately be termed *kidney tubes*, for their function is to withdraw from the blood nitrogenous waste-matters that are the end-products of the series of changes due to the continual breaking-down of the insect's living tissues, whereof the highly complex nitrogen-containing proteins are the characteristic ingredients.

The workings of the various sets of organs in the body are correlated by means of the *nervous system* (Fig. 13), the cells of which can be affected by outside influences and can pass on the "*nerve-impulses*" that they receive so as to evoke suitable responsive action by the muscles or other tissues. Nerve-cells are situated in special *nerve-centres* (or *ganglia*), which in insects are usually small, white, rounded or oval bodies, and these are connected with one another by *nerves* or *nerve-cords*, which are essentially bundles of nerve-fibres, that is to say fine, thread-like outgrowths of the nerve-cells; these fibres, passing from centre to centre, put the nerve-cells in touch with each other.

If the digestive tube of the grasshopper be carefully removed to one side, a great part of the insect's central nervous system will be exposed. Just above the ventral body-wall, a pair of ganglia may be seen lying joined together in the central line in each segment from the first thoracic to the sixth abdominal inclusive, this series (Fig. 13, i, ii, iii, 1–6) of nerve-centres being linked up by a pair of longitudinal nerve-cords that run side by side through the body, while from each ganglion finer nerve-cords run out to muscles and organs belonging to its proper segment. For example, the muscles of the three pairs of legs receive nerves from the three sets of thoracic ganglia respectively, the forewings from the mesothoracic, the hindwings from the metathoracic ganglion. We notice that the hindmost abdominal ganglia (Fig. 13, 6) are larger than the others, and that the four or five hinder segments are innervated from them; hence we infer that these ganglia are complex, built up of several nerve-centres fused together. The system is evidently constructed on the plan of a pair of ganglia for each segment, with the possibility of the ganglia of several adjacent segments becoming united.

This possibility is realized in a high degree in the insect's head. From the prothoracic ganglia the main paired nerve-

cords pass forwards through the neck and become linked with a large *suboesophageal ganglion* (Fig. 13 *sb g*), situated in the head behind the mouth, the centre of nerve-supply for all the jaws and representing therefore the fused ganglia of the three or four hinder segments of the head. From this the two main

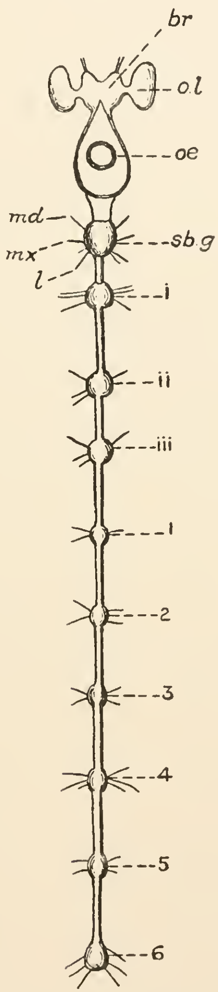



FIG. 13. NERVOUS SYSTEM OF A GRASSHOPPER.
*br*, brain; *ol*, optic lobes; *oe*, gullet; *sb.g*, suboesophageal ganglion; *md*, *mx*, *l*, mandibular, maxillary and labial nerves; *i—iii*, thoracic; 1—6, abdominal ganglia. × 2. In part after Emerton.

nerve-cords may again be traced forwards, passing one on either side of the gullet and joining the very large *brain* (*supra-oesophageal ganglion* Fig. 13 *br*) with several pairs of distinguishable rounded lobes, innervating the eyes and feelers, and representing the ganglia of the foremost two or three limb-bearing segments joined to those of the primitive head-lobes that are formed in front of the mouth in early embryonic development. All the limbs, including the feelers—possibly even the eyes also—are, in the early embryo, behind the mouth, which moves backwards as development proceeds until it comes to lie between the jaws, the mandibles and maxillae.

The nervous system of insects and their allies is particularly interesting to the student of animal-structure because it is so clearly built up on the same segmental plan that is conspicuous in the outer body-form, and because the fusion of successively situated nerve-centres may be traced not only in the development of many an individual insect but also as one compares related insects with one another.

A brief reference to the *reproductive system* may serve to conclude this survey of general insect-structure. In the abdomen of the female grasshopper are situated paired *ovaries*, each ovary (Fig. 14 *o*) consisting of a set of ovarian tubes in which the eggs of the insect undergo their process of growth and ripening. The elongate eggs—subcylindrical in shape with rounded ends—arranged in series along each ovarian tube, give to the tube a beaded appearance, the early eggs towards the narrow ends of the tubes at the dorsal region of the abdomen, are minute ; as each tube is traced backwards and downwards towards its opening it increases in diameter, the contained eggs becoming successively larger (*A*) until the ripened ones are ready for extrusion where the mouths of the ovarian tubes on either side unite to form an *oviduct* (Fig. 14 *od*). The two oviducts open in the mid-ventral line into a median chitin-lined passage, the *vagina* (Fig. 14 *v*), which can be seen externally just in front of the eighth abdominal sternum ; the eggs passing out are seized between the processes of the ovipositor mentioned above. Behind the eighth sternum is seen the opening of a little chitin-lined pouch the *spermatheca* (Fig. 14 *s*), which receives the bundles of sperm-cells from the male in the act of pairing, stores them for a

period, and discharges them as required for fertilizing the eggs as these are laid.

The sperm-cells (or *spermatozoa*) (Fig. 15 *sp*) are minute cells, capable of active motion because the cell-body is drawn out into a long whip-like process or flagellum. They are developed in the male grasshopper's *testes* (Fig. 15 *T*)—small rounded paired bodies situated in the dorsal abdominal region. From

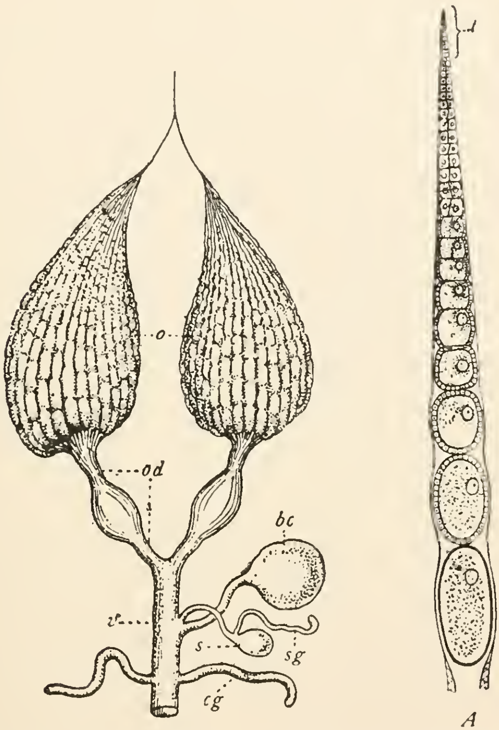



FIG. 14. FEMALE REPRODUCTIVE ORGANS OF AN INSECT.
*o*, ovaries; *od*, oviduct; *v*, vagina; *s*, spermatheca; *sg*, spermathecal gland; *bc*, bursa; *cg*, colleterial glands. Magnified and diagrammatic. *A*, single ovarian tube showing primordial germ-cells in the terminal filament (*t*) and ripe eggs at hinder end. Highly magnified. From Comstock, "Introduction to Entomology".

each testis a delicate tube—the *vas deferens* (Fig. 15 *v d*)—leads backwards and downwards, the two *vasa deferentia* opening into the *seminal vesicles* (Fig. 15 *s v*) composed of a mass of small tubules, whence the chitin-lined *ejaculatory duct* (Fig.

15 *e d*) passes downwards to open on the ninth abdominal sternum. This male reproductive opening is surrounded by a complex set of chitinous processes and hooks known as the *genital armature.*

Our very superficial survey of the adult grasshopper's structure shows that the insect is a creature of great complexity, " highly organized " as the naturalist often expresses it. We have now to consider how this and other animals formed on the same general plan, are built up from simple beginnings, passing in the process through a series of changes. In describing the

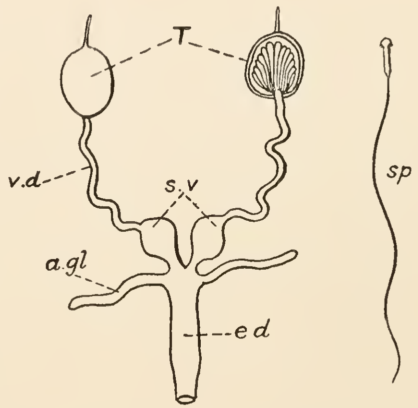



FIG. 15. MALE REPRODUCTIVE ORGANS.
*T*, testes ; *vd*, vas deferens ; *sv*, seminal vesicles ; *agl*, accessory glands ; *ed*, ejaculatory duct. Magnified and diagrammatic. *sp*, a spermatozoon. × 1,500. In part after Comstock.

life-history of any animal, it is convenient to distinguish between the development in the egg or before birth (when the creature is called an *embryo*) and the post-embryonic growth (subsequent to hatching or birth) which may be accompanied by slight or by great changes of form. In our study of growth and change during insect life-histories, it is to the period after hatching or birth that attention will be mainly directed, because the post-embryonic development of insects is such a marked feature in their lives. The embryonic development of insects affords a vast field of study at once difficult and fascinating, so that its adequate treatment would be impossible within

the limits of this book.[1] It must suffice to call attention to a few outstanding facts of insect embryology which will be seen to have a direct bearing on the later development subsequent to the crisis of hatching.

Insects, like other members of the great arthropodan race, produce eggs (Fig. 14 *A*) of large size. The *egg* of any animal is always a relatively large cell in which an amount of food-material for the nourishment of the developing embryo has been stored up during the process of ripening. In certain

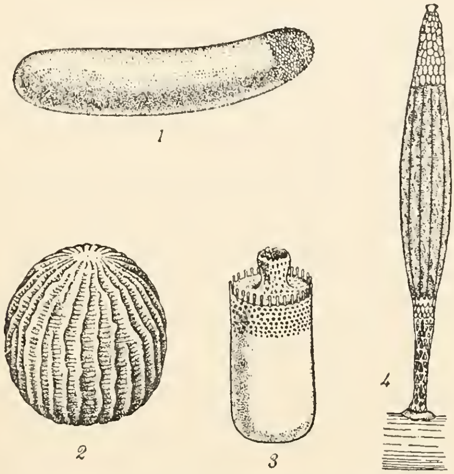



FIG. 16. EGG-CASES OF VARIOUS INSECTS.
1, Cricket (*Oecanthus*); 2, Butterfly (*Oeneis*); 3, Bug (*Piezosternum*); 4, Pond-skater (*Hydrometra*). × 20. From Comstock, "Introduction to Entomology".

groups, however, the mass of this food-material or *yolk* becomes so great that the cell grows into a body easily visible without any microscopic aid. An extreme case of such growth is afforded by the familiar egg of a large bird; here the egg, properly so-called—the overgrown cell—is what is popularly known as the "yolk"; the "white," the membrane, and the shell are to be regarded as a series of successively formed envelopes. Insects, being small animals, cannot produce eggs that are absolutely very large, but relatively to the size of the parent a typical insect egg is large, while compared with the egg of a

[1] R. Heymons: "Die Embryonalentwicklung von Dermapteren und Orthopteren". Leipzig, 1895. J. A. Nelson: "The Embryology of the Honey-Bee". Princeton, 1915.

starfish or a mouse for example, it is enormous, though even such small eggs as those are very large for single cells.

The rich store of food-material in the yolk of an insect's egg is an important factor with regard to the creature's life-history because it ensures that development will have advanced to a considerable extent before the crisis of hatching shall usher the young insect into the surroundings of the outer world. The egg is protected by a firm horny case or shell, which has a characteristic shape and appearance for insects of different groups (Fig. 16). Eggs arise by a series of divisions from the primitive germ-cells, and are at first minute bodies consisting mainly of living protoplasm each with its distinct internal *nucleus* of highly complex structure—the centre of the cell's activities. As growth goes on, yolk accumulates in the cell which, when ripe, is found to have its external region within the envelope mainly protoplasmic while the central mass consists chiefly of inert food-material.

Most insect eggs—as is the case among the vast majority of animals—require to be *fertilized* before they begin to develop. The essential process of fertilization is the entrance into the egg of the head of a spermatozoon or active, vibratile sperm-cell, large numbers of which are received into the female's spermatheca when she pairs with a male. The head of the spermatozoon consists chiefly of the *sperm-nucleus*, which uniting with the *egg-nucleus* forms the *zygote-nucleus* whence all the nuclei of the myriad cells that build up the body of the offspring are derived by repeated series of divisions. There are, however, a large number of cases now known among insects in which the egg is capable of development without fertilization ; these afford examples of *parthenogenesis* or virgin-reproduction. The numerous successive generations of aphids or " greenfly " during spring and summer, which are all females, and the " drones " of the hive-bee and many related insects, which are males, arise from parthenogenetic eggs. Many highly interesting problems of inheritance have been elucidated by recent researches on the details of nuclear behaviour during the maturation of the germ-cells and the fertilization of the eggs in various insects.[1] But without pausing to discuss

[1] L. Doncaster : " An Introduction to the Study of Cytology ". Cambridge, 1920.

these, we must pass to the outline of those processes by which the body of the young insect is built up within the egg.

The development of any living creature from an egg is brought about by successive cell-divisions, so that the multitudinous cells which build up the body of the new animal may be regarded as descendants of the original egg-cell. We have seen that in an insect's egg the living protoplasm surrounds, for the most part, a central yolk. Consequently the preliminary cell-divisions leading to what is known as the *segmentation* of the egg take place in the active external protoplasmic region,

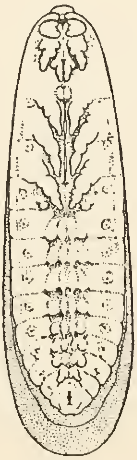


FIG. 17. EMBRYO OF WATER-BEETLE (*Hydrophilus*). Ventral view showing developing segmentation of body with appendages, and amnion. × 30. From Comstock after Heider.

resulting in the formation of an enveloping sheet of cells (the *blastoderm*) around the central mass of food-yolk.

Along one face of the segmenting egg the blastoderm becomes thickened forming the *germ-band*, the position of which marks the ventral region of the embryo. In the germ-band the cells become differentiated into an outer and an inner layer. The outer layer (or *ectoderm*) gives rise to the skin (or epidermis), the nervous system, the linings of the air-tubes and of the fore- and hind-guts as already mentioned. From the inner layer are derived all the other organs of the body

as various groups of cells become more and more differentiated for special purposes. In the development of most insects, the thin blastoderm surrounding the germ-band, grows in such a way as to form a protective sheet or *amnion* over the latter in which the main features of the body-form are progressively marked out (Fig. 17). The segmentation of the body is indicated by transverse furrows across the germ-band. At a very early stage, primitive head- and tail-regions may be distinguished, and the series of limb-bearing segments are formed in regular order from before backwards, so that the tail-region is pushed farther and farther from the head as growth proceeds. In each segment there may be present a pair of nerve-ganglia, and a pair of cavities (*coelomic spaces*) in the *mesoderm* tissue derived from the inner cell-layer, while on each segment a pair of limbs or appendages may grow out. The last-named structures may, as the legs of the embryo grasshopper, cockroach, or bug, grow so rapidly that by the time of hatching they resemble closely those of the adult ; or they may remain in a rudimentary condition, as for example do the thoracic legs of certain beetle-grubs ; or they may, after having attained slight development disappear entirely before hatching, as is the case with the rudimentary limbs on the anterior abdominal segments of other beetle embryos.

The inpushings of the ectoderm to form the front- and hind-regions of the food-canal appear at an early stage in the mid-ventral line of the germ-band, the opening of the fore-gut—the future mouth—just behind the primitive head, and that of the hind-gut on the primitive tail-region. As growth proceeds the mouth moves backwards from its original position in front of the feelers to its final place behind the mandibles and between the maxillae. The fore-gut and hind-gut grow inwards to communicate with the insect's central digestive cavity in which the store of food-yolk, enclosed by the growth of the embryo, is gradually absorbed.

The close of embryonic development leads on to the important operation of hatching which ushers the young insect into its free, active life. The details of the hatching process vary greatly among insects of different groups, and some of these will be mentioned in subsequent pages of this volume. For the present it may suffice to describe briefly the emergence of the

young of such a grasshopper or locust as that whose fully developed form has been summarized in this chapter. The female of such an insect works her abdomen quickly but carefully into the ground, and lays her eggs in the soil (Fig. 18 A, B),

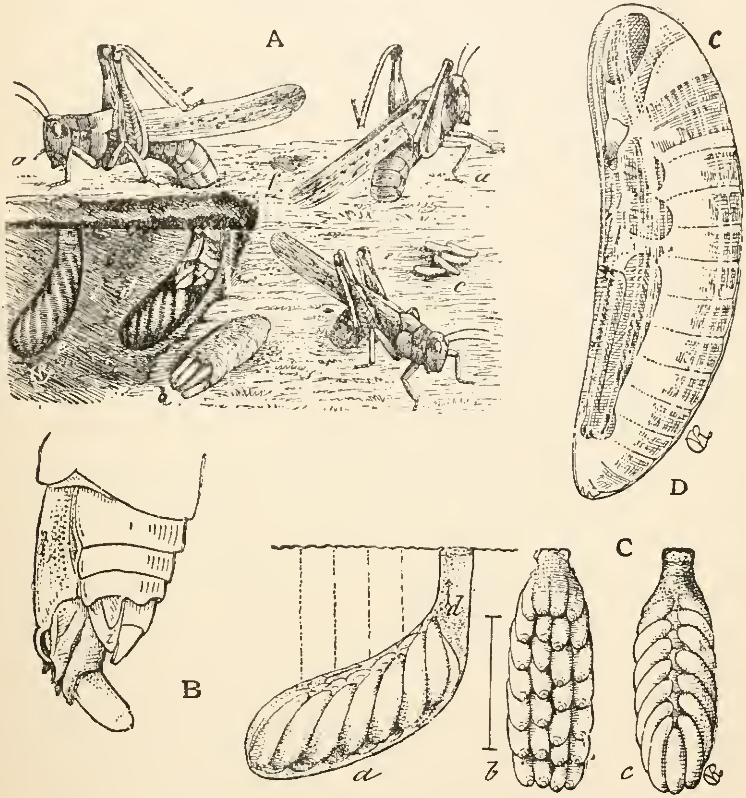



FIG. 18. EGG-LAYING OF THE ROCKY MOUNTAIN LOCUST (*Caloptenus spretus*).
A, Females (*a a*) depositing their egg-clusters (*d e*) in the soil; *b*, an egg-cluster; *c*, scattered eggs on the surface. Natural size. B, Tip of female's abdomen showing ovipositor holding egg; × 3. C, Egg-clusters; *a*, side view; *b*, from beneath; *c*, from above. × 3. D, Embryo enclosed in amnion (note the long hind-leg), cervical ampulla at *c*. × 20. From Riley, *Entom. Bull.* 25, *U.S. Dept. Agric.*

surrounding them with a gelatinous secretion which, by fastening together particles of earth, builds up a tubular egg-case closed at the top by a lid. When the young locusts emerge from the egg-shells they present an extensive dorsal area of flexible cuticle (Fig. 18 D*c*), behind the head and in front of the

prothorax ; by means of increased blood-pressure in this neck-region the thin cuticle is made to protrude like a bladder. Six or seven of the baby-insects thus unite their efforts and succeed in raising the lid and making their way between the crevices of the soil into the upper air. But although free from the egg-shells and their tubular case, each little locust is still enshrouded in its amnion (Fig. 18 D). The cervical bladder is therefore again brought into use, by its protrusion bursting the amnion which the insect slips over its head, afterwards withdrawing the legs and abdomen. In some cases the young locust demonstrates its new-found independence of embryonic trammels by kicking the empty amnion away with its hind feet.

Thus freed from egg-shell, egg-case and amnion the little grasshopper (Fig. 19 *a*) is started on its open life in the world. A brief examination suffices to demonstrate its close likeness to its parent in essentials of form. The head is of the same shape and although the feelers are relatively shorter than those of the adult and have fewer segments the structure of the jaws is almost exactly the same, and naturally also are the kind of food and the mode of feeding. The legs are almost miniature reproductions of the parent's limbs, those of the third pair having attained their characteristic elongation before hatching (Fig. 18 D) so that they enable the young grasshopper to leap relatively far and high as soon as it has thrown off the enveloping amnion. Each foot, as in the adult, has three segments. As previously mentioned, the newly-hatched insect differs conspicuously from its parent in the total absence of wings, and together with this deficiency goes a want of specialization in the exoskeleton of the thoracic segments ; as none of them bear wings, they show but slight differentiation, and with the exception of the prothorax, resemble generally the segments of the abdomen. Another less conspicuous but noteworthy distinction between the adult and the newly-hatched young is found in the hinder abdominal segments, the characteristic reproductive processes being as yet not apparent.

During its development to the adult condition the grasshopper has to undergo five of those moults or castings of the cuticle, which have already been indicated as essential to the accomplishment of growth among insects. Before a moult

(or *ecdysis*), the skin separates from the cuticle, a fluid secreted by cells of the skin occupying the intervening space. On the surface of the skin a new cuticle begins to form and, while this has generally the structure of the old, new features may be introduced by outgrowths of various regions of the body, which being covered by skin will have the outermost coating or cuticle formed over them. Thus during a new stage in the life-history, the insect may differ appreciably, if slightly, from its condition in the preceding stage. For the accomplishment of each moult, the cervical bladder, between the head and prothorax, already mentioned as effective in the processes of hatching and casting of the amnion, is again brought into use. By the pressure of this bladder the dorsal cuticle is split lengthwise and through this split, the insect, clad in the new cuticle which has formed beneath the old one, carefully extricates its body and limbs. First the head and prothorax are withdrawn, then the feelers, then successively the first and second and third pair of legs, and finally the abdomen. The new *instar* (a convenient term for an insect in any one stage of its life-story) is larger than the former one, but the body within the old cuticle has been contracted and the skin folded. Now by swallowing air and increasing the blood-pressure, not only is the old cuticle split, as we have seen, but the newly-emerged instar expands, and it follows that the new cuticle when—through deposit of the lower "secondary" layer beneath the first-formed "primary" sheet (see Fig. 2)—it has become in the exoskeletal parts, thick and firm, is found to be more extensive than the old. Thus through its succession of moults the insect grows in size and may also change in form.

The second instar of the grasshopper (Fig. 19 *b*) shows increase in bulk as compared with the newly-hatched insect, but no marked change in structure. There is as yet no trace of wings, and the thoracic segments are still closely similar, though the foremost (prothorax) shows a slight relative increase in length when compared with the other two. After the second moult, when the third stage (Fig. 19 *c*) in the life-history has been reached, the prothorax begins to assume the prominent hood-like aspect which characterizes it in the adult, and the *wing-rudiments* on the mesothorax and meta-

thorax are plainly visible, having grown out from those segments beneath the cuticle of the preceding instar before the moult took place. These wing-rudiments are, at this stage, merely rounded lobes on the hind dorsal region of the segments to which they belong, traversed by diverging track-lines which indicate the position of air-tubes marking out generally the course of the future wing-nervures.

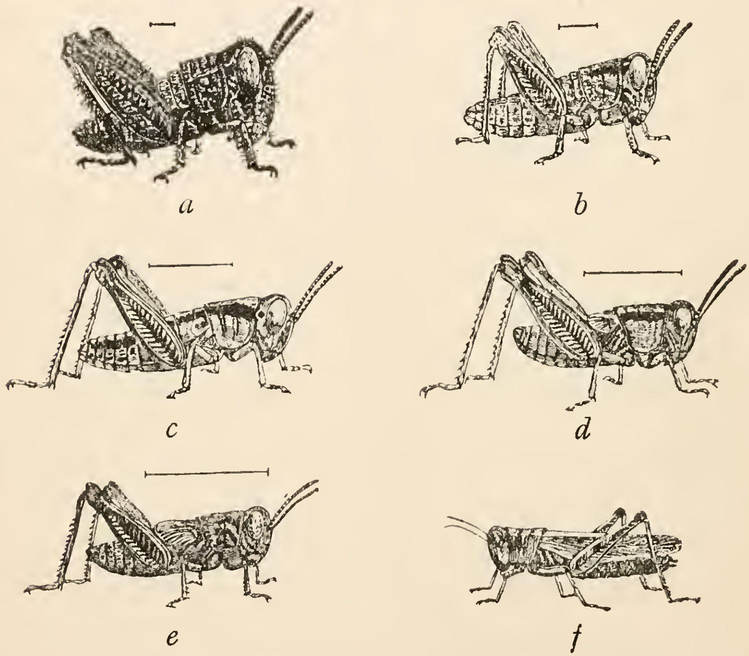


FIG. 19. SUCCESSIVE STAGES IN THE GROWTH OF A GRASSHOPPER (*Melanoplus*).
*a*, first instar; *b*, second instar; *c*, third instar with minute wing-rudiments; *d*, *e*, fourth and fifth instars with distinct wing-rudiments. Magnified (natural size indicated in each case by the index lines). *f*, Adult. Natural size. From Comstock, "Introduction to Entomology", after Emerton.

With the assumption of the cuticle of the fourth stage (Fig. 19 *d*), the wing-rudiments are seen to be much more prominent than before, no longer mere lobes on the mesothorax and metathorax, but imperfectly jointed to those segments, looking like miniature wings with the developing nervuration distinctly visible. The general form of the fifth instar (Fig. 19 *e*) closely resembles that of the fourth, but the wing-

rudiments are larger, the costa of the forewing equalling, in some cases, the prothorax in length. This stage is the last but one, being followed by the final, fully-winged *imago* (Fig. 19 *f*) or perfect insect.

Although the grasshopper's development after hatching pursues a regular and even course, unmarked by any striking change, the assumption of the final, winged condition is a noteworthy episode. The last moult is brought about in the same manner as the preceding ones; the old cuticle splits dorsally lengthwise, and the head and thorax of the new instar are disengaged first, then the front and the middle legs and the wings, then the abdomen and hindlegs, the latter


FIG. 20. THREE STAGES (*a*, *b*, *c*) IN THE EMERGENCE OF THE ADULT ROCKY MOUNTAIN LOCUST (*Caloptenus*) FROM THE LAST NYMPH-CUTICLE.

In *c*, the insect has reversed its position and the wings are drying. Natural size. After Riley, *Entom. Bull.* 25, *U.S. Dept. Agric.*

being sharply flexed at the knee-joint, so that the shin lies close against the thigh. Before this moult, the insect has climbed to a shoot of some convenient plant to which it clings by its feet, and the winged instar emerges so that it hangs almost vertically head downwards (Fig. 20 *a*), only the hinder region of the abdomen remaining within the old cuticle; in this position, the abdomen becomes distended through the absorption of air, and attains its full length. Before the withdrawal of the tail region from the old cuticle, the abdomen is strongly bent, so that the feet of the front and middle legs can grasp the plant-shoot up which the former instar had previously crawled. Then the emergence is completed, and

the newly-revealed imago rests with its head above, its abdomen and wings hanging downwards, while the cuticle undergoes the final stretching and hardening processes (Fig. 20 *c*).

The changes connected with the wings are of especial interest. The cuticle which covers these organs has been formed within the wing-rudiments of the preceding instar previously to the moult, and as these rudiments extend only to about a third of the length of the abdomen, the enclosed wings must necessarily be crumpled and folded. When first withdrawn from the old cuticle, they are straight and parallel to the abdomen, but as the imago hangs head downwards, and the blood and air pass into the wings so that they begin to expand and stiffen, this operation progressing from the bases onwards, their tips bend down—so that they assume a procurved position over the thorax (Fig. 20 *b*). Then, as by the bending of the abdomen (Fig. 20 *c*), the head of the insect becomes directed upwards and the abdomen points downwards, the wings, continuing to expand, assume again the normal position parallel to the abdomen which they exceed in length when they have attained their full size. It is noteworthy that at first the costa of the wings is directed dorsalwards, and that the broad hindwings, as yet unfolded, lie external to the narrower and longer forewings. But, as the wing-cuticle attains its ultimate firm and hard texture, these positions become reversed ; through a basal torsion, the wings of both pairs come to have the costa directed ventralwards, and the hindwings, their delicate areas folded fanwise, are brought to a position between the forewings which serve to cover and protect them (Figs. 1 B 19 *f*).

Briefly surveying the course of the grasshopper's life-history, we note that the newly-hatched insect closely resembles its parents, that through its subsequent development it lives and feeds in much the same way, being active in every period of its growth, and that the wing-rudiments appear outwardly at an early stage and increase in size after each moult, with somewhat sudden advances however in the fourth and final instars. These facts will be found of importance for comparison with those displayed in the life-histories of other insects.

In this introductory survey of the life-history of some typical insects, we may pass from that of a grasshopper to that of a dragon-fly, and it will be again convenient to preface discussion of the young stages with a brief, general account of the structure of the adult insect.

A typical dragon-fly (Fig. 21) is one of the most remarkable of all insect-forms. In these insects we have, to quote a recent authority,[1] "a singularly isolated group, marked by

FIG. 21. DRAGON-FLY (*Aeschna cyanea*).
Natural size. From Latter "Nat. Hist. of Common Animals".

very high specializations of structure, superimposed upon an exceedingly archaic foundation." The dragon-fly's head is broad and prominent, very freely movable on the prothorax, a large proportion of its area occupied with the great sub-globular compound eyes, besides which three simple eyes (*ocelli*) are present, situated in the centre of the crown. The feelers are short and slender, almost thread-like, with at most

[1] R. J. Tillyard: "The Biology of Dragon-flies". Cambridge, 1917.

seven segments. The mandibles (Fig. 22 A, B) are stout and strong with an armature of formidable teeth adapted for the predaceous habits of the insect, which feeds greedily upon

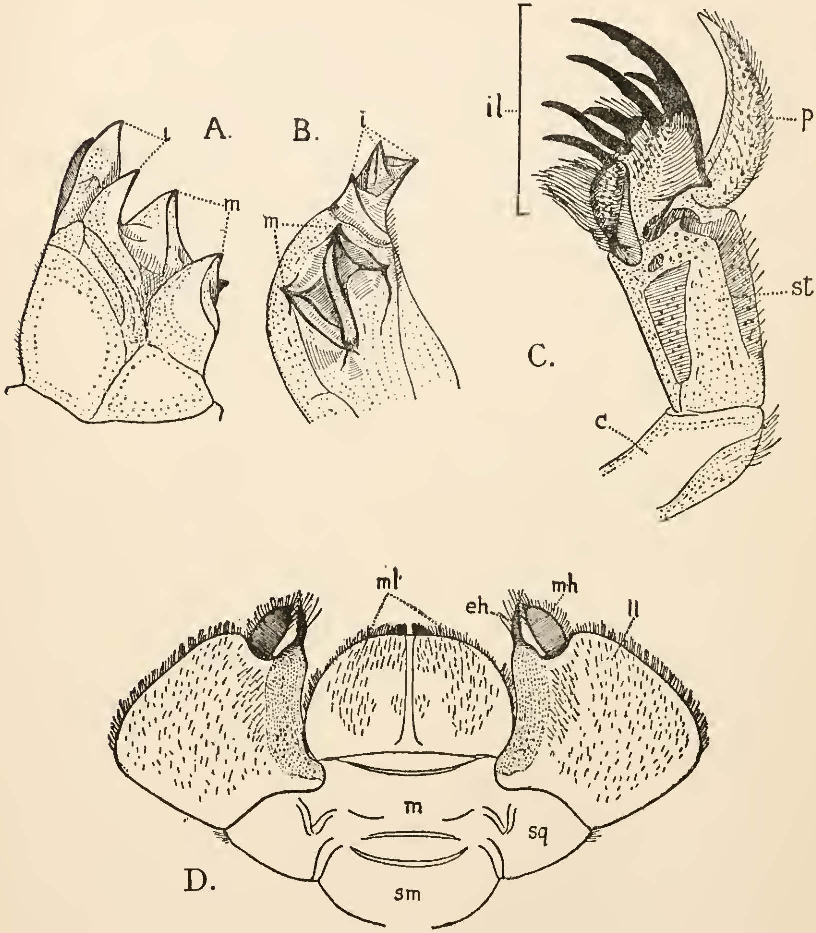



FIG. 22. JAWS OF DRAGON-FLY (*Aeschna*).

A, Mandible (outer view); B, inner view; *i*, apical teeth; *m*, molar teeth. C, Maxilla; *c*, cardo; *st*, stipes; *p*, palp; *il*, lobe (galea and lacinia). D, Labium; *sm*, sub-mentum; *m*, mentum; *sq*, squame; *ll*, palp; *eh*, end hook; *mh*, movable hook; *ml*, median lobe (galeae and laciniae). × 12. From Tillyard, "Biology of Dragon-flies".

weaker members of its class caught in flight. In the maxilla (Fig. 22 C), the galea and lacinia are fused to form another formidably-toothed structure, while the crescentic hairy palp

(*p*) is unjointed. The labium (Fig. 22 D) is wide and flattened with a broad mentum (*m*) which carries a median plate (*ml*)—in some cases clearly composed of paired elements (perhaps both *galeae* and *laciniae*) fused together—and a pair of curiously-modified palps, each with two segments (Fig. 22 C *ll*, *mlh*), the basal of which is exceedingly broad.

The dragon-fly's thorax is strangely modified, the pleural areas of the segments are extensive, so that the body is deep in proportion to its width, and strongly oblique so that the sternal region bearing the legs is thrown forwards towards the head, and the tergal region where the wings are inserted reaches backwards towards the abdomen (Fig. 21). The prothorax is distinct, while the mesothorax and metathorax are somewhat closely united together. The legs are strong though slender, the thighs and shins armed with rows of sharp spines closely arranged; as the legs can all be held under the head and beneath the mouth, they form an efficient fly-trap for the capture of the small insects that form the dragon-fly's prey. Each foot, as in the grasshopper, has three segments, the terminal one bearing two claws. Unsuitable for walking on the ground, the dragon-fly's legs are admirably adapted for clinging and climbing on plants. The wings are firm and glassy in texture, those of the two pairs closely alike both in form and in their very complex and characteristic nervuration. Dragon-flies are insects with great powers of flight, and the wing musculature is very strong, the muscles for depressing or raising the wings being connected by means of firm tendons to specially-developed sclerites attached to the wing-bases.

The abdomen is elongate and usually slender, though in one well-known group of dragon-flies (the *Libellulinae*) it is comparatively broad. The male has, on the second and third abdominal segments, a remarkable and complex armature for pairing, an arrangement found in no other group of insects. The female has an ovipositor composed of three pairs of outgrowths on the eighth and ninth abdominal segments corresponding to those of the grasshopper. This ovipositor is well developed in those dragon-flies that cut slits in water-plants wherein to lay their eggs, but in large sections of the order the eggs are simply dropped into water and the ovipositor is in a reduced or degenerate condition. At the hinder end

of the abdomen a pair of strong unjointed appendages are present in both sexes ; these are especially large in the male, which uses them in pairing, in conjunction with one or two lower processes which are wanting in the female.

The digestive system (Fig. 25 A) of a dragon-fly has the same parts and the same general arrangement as that of a grasshopper ; the stomach (*mg*), however, is relatively longer and the intestine (*hg*) relatively much shorter, for the whole food-canal runs a straight course from mouth to anus, such abbreviation being a well-known modification in animals which live on flesh-food rather than on vegetable matter. In the nervous system (Fig. 26 A) the great brain (*br*), with its strongly-developed optic ganglia (*og*), is noteworthy. The thoracic ganglia (*tg*, 1, 2, 3) are close together, the first abdominal (*ag* 1) being almost in contact with the third thoracic, and being followed by a chain of seven other abdominal ganglia (*ag* 2-8). The large compound eyes have already been mentioned, and dragon-flies are said to be more far-sighted than any other insects. In correlation with their powerful flight and high activity, dragon-flies have especially-developed breathing organs. Large paired dorsal and ventral trunk air-tubes (Fig. 25 A, *dt*, *vnt*) run along the body, from head to tail, and there are also a pair of visceral trunks (*vt*) lying alongside the food-canal. The tubes receive the air supply through ten pairs of lateral spiracles, a pair on the mesothorax, a pair on the metathorax, and a pair on each abdominal segment from the first to the eighth inclusive (Fig. 25 A, *sp*). The whole build of a dragon-fly—the mobile head with its great eyes and strong jaws, the spiny legs, the long, firm wings, the well-poised hind-body—suggests adaptation for life in the air.

Turning to the life-history of such an insect, we are struck by the fact that its early stages are passed under water, and thus it is clear that the conditions amid which the young creature lives must be very different from the aerial surroundings of the winged adult, and it is evident that its body-form must differ correspondingly. It has already been mentioned that some female dragon-flies lay their eggs in slits cut by the ovipositor in the tissues of aquatic plants, while others simply drop them into the water. The embryonic

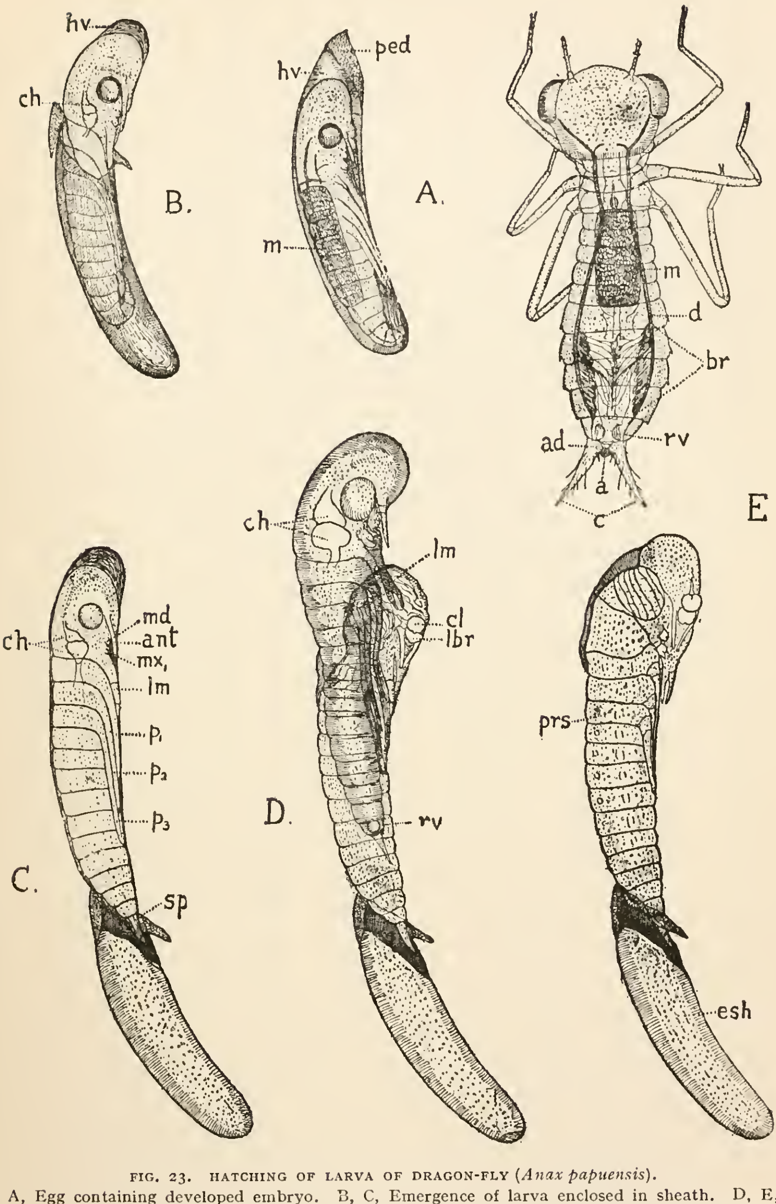



FIG. 23. HATCHING OF LARVA OF DRAGON-FLY (*Anax papuensis*).

A, Egg containing developed embryo. B, C, Emergence of larva enclosed in sheath. D, E, Emergence of larva from its sheath. *ped*, stalk of egg; *hv*, head-vesicle; *ch*, cephalic heart; *m*, stomach; *cl*, face; *lbr*, labrum; *ant*, feeler; *md*, mandible; *mx*, maxilla; *lm*, labium; $p_{1-3}$, legs; *rv*, rectal valves; *ad*, dorsal appendix; *a*, anus; *br*, branchial basket; *d*, dorsal air-trunk; *esh*, egg-shell; *prs*, empty sheath. ×30. From Tillyard, "Biology of Dragon-flies".

development of the dragon-fly cannot be traced in detail here, but there is an interesting variation from that of the grasshopper in that the germ-band grows so as to be folded into the yolk, carrying with it a sheet of thin blastoderm which forms the amnion, and lying for a while with its ventral aspect towards the face of the egg opposite to that along which it was originally formed. Then at a later stage, the embryo reverts to its original position, bursting the amnion in the process, and before hatching secretes a thin, firm cuticle which ensheathes the appendages already definitely formed. The egg-shell is ruptured (Fig. 23 A, B) by the swelling of the head region of the embryo due to the action of a pulsating " cephalic heart " (Fig. 23 *ch*) connected with the gullet ; thus the young insect enswathed in its cuticular sheath is hatched. In a few minutes, or possibly in a still shorter period, by the continued action of the " cephalic heart," this sheath may be burst, and the larva creeping therefrom is ready to begin its active life (Fig. 23 C, D).

The young larva of a dragon-fly (Figs. 23 E, 24) has a broad head with a pair of compound eyes already fairly prominent, and short three-segmented feelers. The three thoracic segments are closely alike with the legs relatively very long, each foot consisting of a single segment bearing two claws. The abdomen is short compared with that of the adult, broad in the larvae of the more robust and larger dragon-flies, slender in the young of the delicate damsel-flies (or " demoiselles ") ; at the tail end are a pair of fringed appendages, and sometimes a median one also. Turning again to the head, we notice that the mandibles and maxillae are much like those of the adult dragon-fly, but the labium is remarkably modified. The sub-mentum and mentum (Fig. 24 *sm*, *m*) are both elongated, the latter hinged to the former and the former to the ventral head skeleton ; thus the organ can be folded so as to be hidden beneath the head (Fig. 24 B, C, E), or can be stretched out far in front of it (Fig. 24 D). At the extremity of the mentum is a median lobe (Fig. 24 D, *ml*, probably representing both *laciniae* and *galeae*) and a pair of externally-placed, jointed, sharp, toothed processes (Fig. 24 D, *mh*), the modified palps. By means of these, when the " mask " (as this strangely transformed labium is called) is stretched out, the

larva is able, lurking at the bottom of its native pond or stream, to seize as prey any smaller or weaker insect that happens to pass within its reach ; and when the mask is again drawn back, the prey is brought within reach of the mandibles

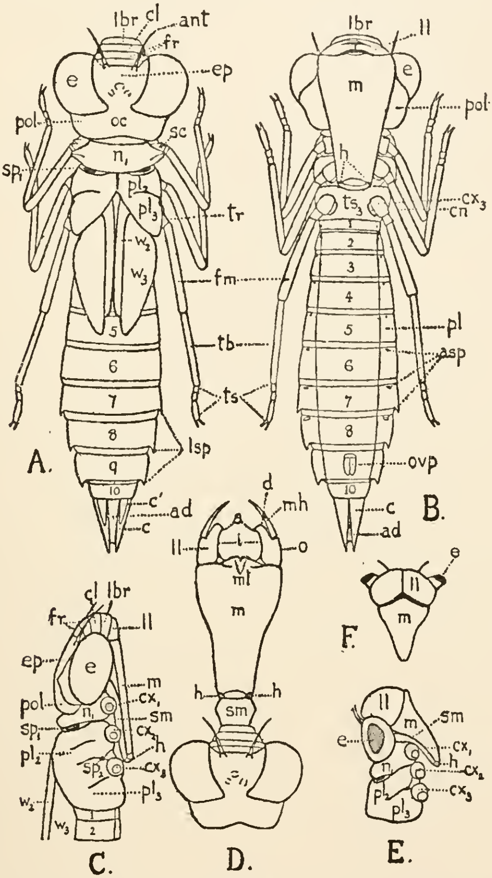



FIG. 24.

A—D, Nymph of Dragon-fly (*Aeschna*). A, dorsal view; B, ventral view; C, lateral view of head and thorax with mask retracted; D, dorsal view of head with mask extended; E, head and thorax of larva of *Tramea*, lateral view; F, head of same, front view; mask retracted. × $1\frac{1}{2}$. *ant*, feeler; *ep*, crown of head; *fr*, frons; *cl*, face; *lbr* labrum; *oc*, occiput; *e*, eye; *pol*, postocular lobe; *sm*, submentum; *m*, mentum; *h*, hinge of labial mask; *ll*, lateral lobe (palp); *a*, *d*, its hooks; *ml*, median lobe (galeae and laciniae); *n*, pronotum; $pl_2$, $pl_3$, meso- and meta-thorax; *cx*, haunches; *tr*, trochanter; *fe*, thigh; *th*, shin; *ts*, foot; $w_2$, forewing rudiments; $w_3$, hindwing rudiments; *sp*, spiracles; 1—10, abdominal segments; *c*, cercus; $c_1$, upper appendage; *ad*, dorsal appendix of abdomen; *ovp*, ovipositor. From Tillyard, "Biology of Dragon-flies".

so that it may be bitten up and devoured. Hence the larva is, like the adult, a predaceous creature, but the adaptation for securing victims is widely different, for while the adult catches flies as it skims through the air, the larva rests in its watery home as a comparatively sluggish stalker, waiting, with mask folded beneath the head, for a suitable prey to pass by its lair.

Through a series of ten to fourteen moults the young larva grows towards the adult condition ; the time occupied by these changes may be one or two—in some cases even three to five—years. The compound eyes increase in size and in the number of their facets after each moult, but the ocelli do not appear until the latest stages. The mesothorax and metathorax increase in size while the prothorax remains relatively small ; after the second moult each foot becomes two-segmented, and somewhat later (Fig. 24) the third segment is added. Wing-rudiments (Fig. 24 A C, *w2*, *w3*) are clearly visible about the fifth stage, and these become larger after each moult ; they are triangular in form lying obliquely over the front of the abdomen, and so arranged that the hindwing overlaps the forewing on each side. Thus it comes to pass that the upper surface of the larval wing-rudiment becomes the lower surface of the developed wing in the adult dragon-fly.

With regard to the internal organs of the larvae, it may be noted that the ganglia of the central nervous system are relatively very large and very close together in the newly-hatched insect (Fig. 26 B). As growth proceeds the nerve-cords lengthen so that the ganglia, hardly increasing in size, become far apart from one another. The digestive system of the larva shows the same general arrangement as that of the imago, but the mid-gut is relatively shorter and the hind-gut longer. In larvae of the larger and more robust dragon-flies, the central region of the hind-gut is enlarged and specialized to form the curious breathing organ known as the *branchial basket.*

In this remarkable structure we see one of the special adaptions necessary for the dragon-fly larva's life under water. In the aquatic habit of its larva, a dragon-fly resembles many other insects of various orders, and the diverse modifications that enable such larvae to breathe afford one of the most

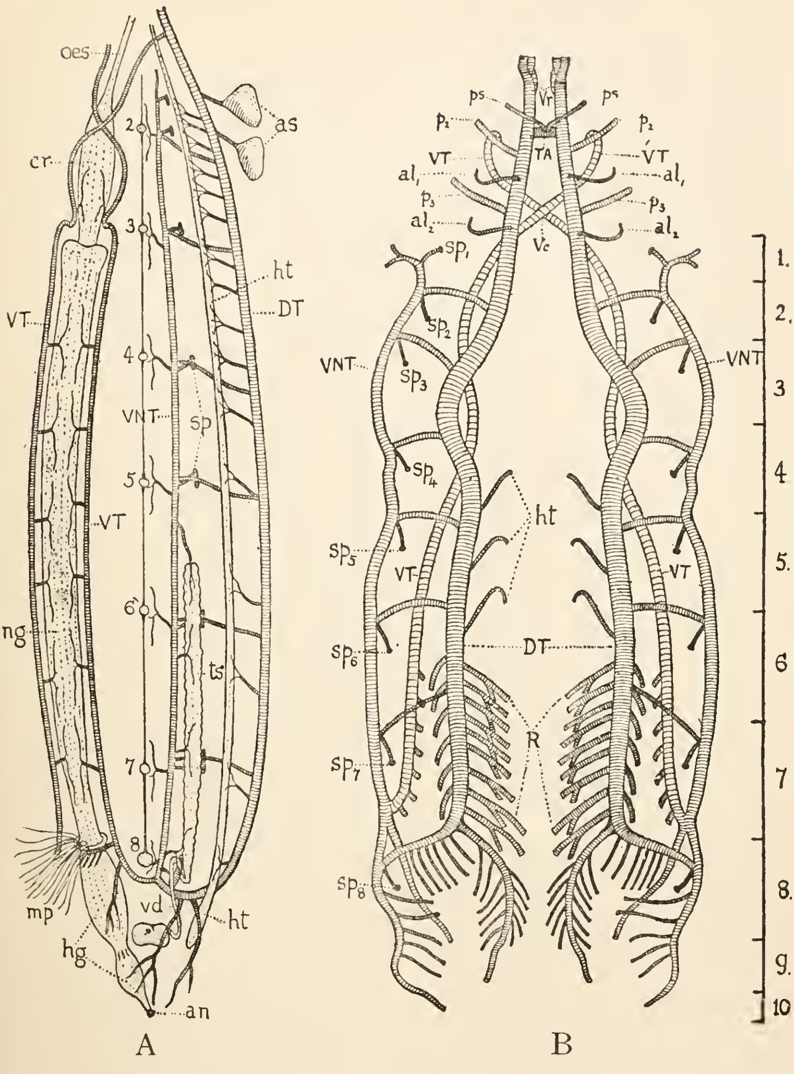



FIG. 25.

A, Internal Anatomy of Male Dragon-fly (*Aeschna*). Heart (*ht*) displaced to right, food-canal (*oes*, gullet; *cr*, crop; *mg*, stomach; *hg*, intestine; *an*, anus; *mp*, kidney-tubes) displaced to left; *VT*, visceral air-trunks; *DT*, right dorsal, and *VNT*, right ventral air-trunks (left ones removed); *sp*, spiracles; *as*, air-sacs; 2—8, nerve-ganglia; *ts*, right testis (the left removed); *vd*, vas deferens. ×2½. B, Tracheal System of *Larva of Dendroaeschna*. *Vr*, visceral remnant; *TA*, thoracic anastomosis; *ps*, thoracic spiracular tube; $al_1$, $al_2$, trunks of wing-rudiments; *Vc*, visceral crossing; $p_2$ $p_3$ trunks if legs; *ht*, air-tubes of heart; *R*, tubes from rectal gills ("branchial basket"); 1—10, indicate position of abdominal segments. Other references as in A. × 6. From Tillyard, "Biology of Dragon-flies".

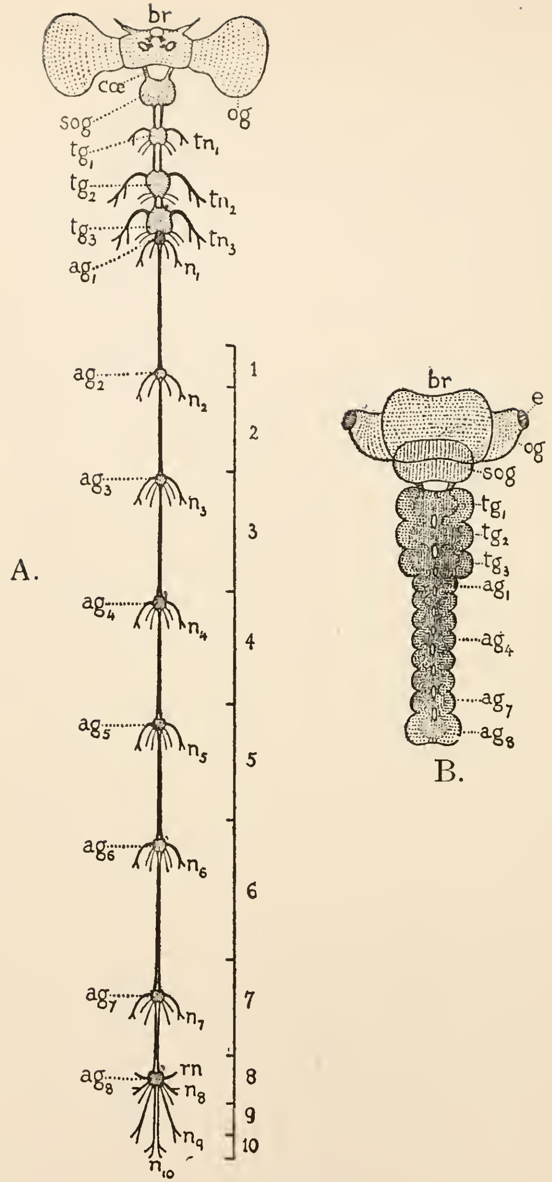



FIG. 26.

A, Nervous System of Dragon-fly (*Petalura gigantea*). *br*, brain ; *coe*, connectives ; *sog*, sub-oesophageal ganglion ; $tg_{1,\,2,\,3}$, thoracic ganglia ; $tn_{1,\,2,\,3}$, thoracic nerves ; $ag_{1}$—$_{8}$, abdominal ganglia ; $n_{1}$—$_{10}$, abdominal nerves ; 1—10 shows outer limits of abdominal segments. ×2. B, Nervous System of Newly-hatched Dragon-fly Larva (*Diplacodes haematodes*). *e*, eye ; *og*, optic ganglion (other references as in A). ×53. From Tillyard, "Biology of Dragon-flies".

fascinating bypaths of nature-study. The dragon-fly larva possesses, like insects generally, a system of air-tubes (Fig. 23 E *d*, 25 B), but while it lives submerged in water there is no direct access to this system from without ; the abdominal spiracles (Fig. 25 B *sp.*) are closed, and those on the thorax alone may remain open, to become possibly functional on occasions when the larva will leave for awhile its watery home and make preliminary trials of the atmosphere, on aquatic plant-stems or half-submerged rocks. But while the insect is submerged it depends for its supply of oxygen on the air dissolved in the water, and this is made available by means of special sub-aqueous breathing organs (or *gills*). As just mentioned these gills are found, in the larger and more robust dragon-flies, on the inner wall of the large central chamber of the hind-intestine known as the branchial basket (Fig. 23 E *br*). Outgrowths of the wall in form of undulated plates or finger-like, thread-like, or leaf-like lobes (Fig. 27 A-F) project into the cavity, and these enclose fine air-tubes which are connected (Fig. 25 B, *R*) with the great paired dorsal (*DT*) and ventral (*VNT*) trunks. Into these oxygen is diffused from the dissolved air of water taken into the hind-gut, and the periodical forcible ejection of this water assists the larva in locomotion by urging it forwards as by the working of a jet-propeller.

The larvae of the slender, delicate damsel-flies also are able to breathe through the wall of the hind-gut, though it has no specialized gill-outgrowths. These larvae are provided however, with other organs of respiration in the tail-process and the paired appendages (*cerci*) at the tip of the abdomen, which are modified into external gills (Fig. 27 G H), circular or compressed in cross-section, and traversed by numerous fine branching air-tubes.

Thus the dragon-fly larva lives in its underwater world, growing towards the adult condition through its successive moults as regards the increase in size of its eyes and of its wing-rudiments, so that during its later stages it is often spoken of as a *nymph*. But the characteristic larval structures —the mask and the gill-system—persist in the penultimate instar, so that the final moult which results in the emergence of the winged adult involves a real transformation. The ripening nymph suffers atrophy of its gills, and thrusting the front

regions of its body out of the water breathes atmospheric air through the now open thoracic spiracles. Beneath the old cuticle, the new imaginal cuticle is formed, causing some striking changes in appearance and colour. At length the nymph crawls up some water-plant ; the internal growth goes

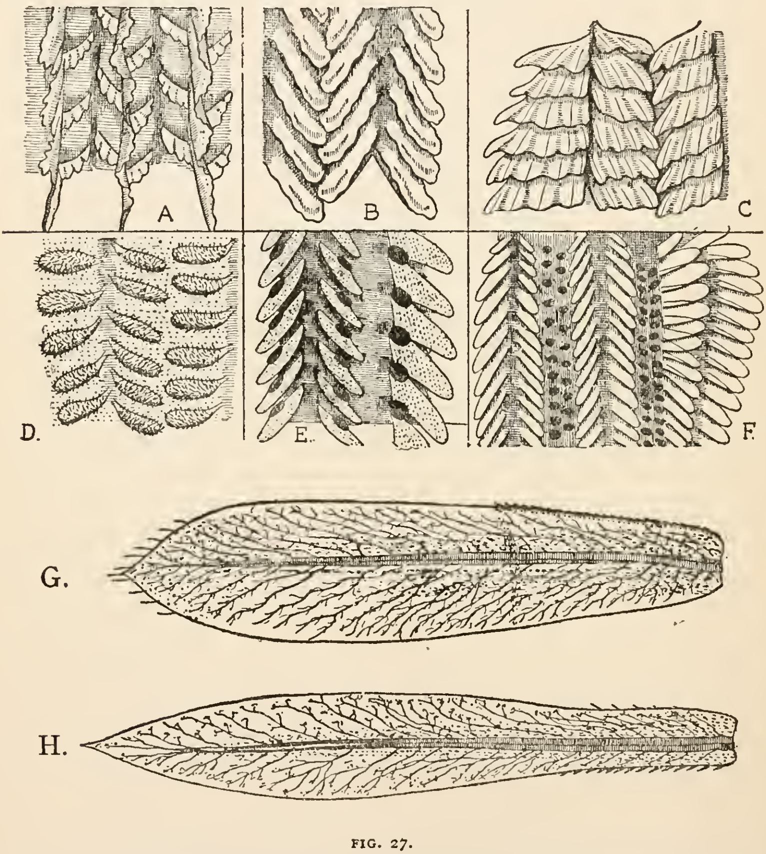
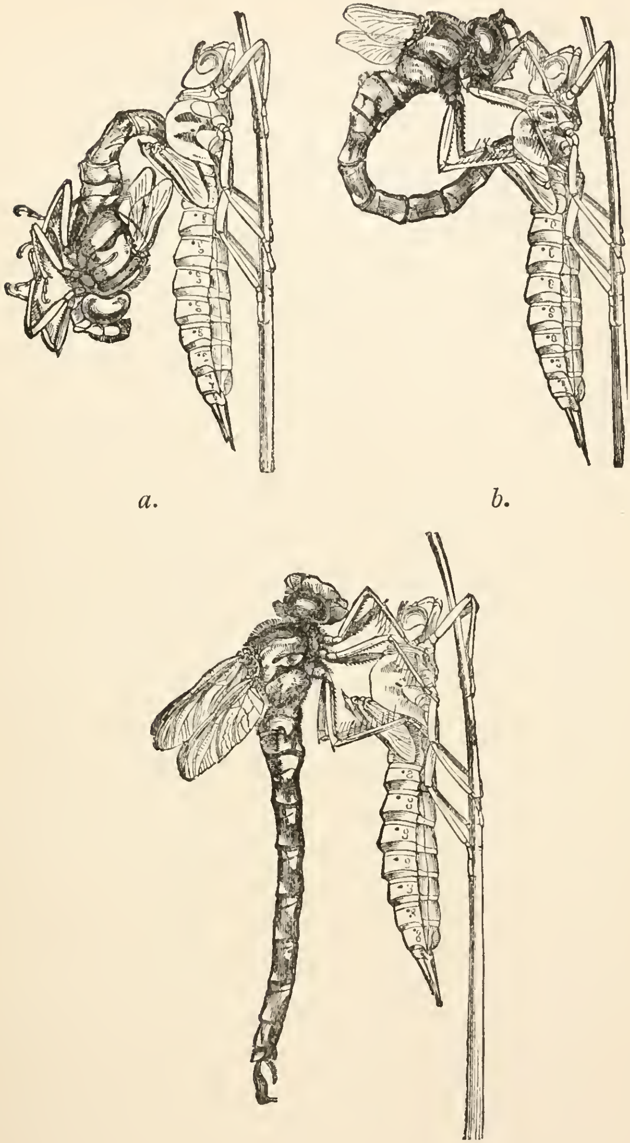



FIG. 27.

A—F, Forms of rectal gills of dragon-fly larvae. ×10. A, *Austrogomphus* (undulate type) ; B, *Austroaeschna* (implicate type) ; C, *Aeschna* (foliate type) ; D, *Anax* (papillo-foliate) ; E, *Synthemis* ; and F, *Diplacòdes* (lamellate) ; G, H, Caudal gills (modified cerci) of Damsel-fly larvae. ×12. G, *Ischnura* ; H, *Agriocnemis*, showing air-trunks with branching tracheoles. From Tillyard, " Biology of Dragon-flies ".

on so rapidly that the cuticle of the nymphal thorax splits along the mid-dorsal line, and the fly withdraws first the thorax, then the head and legs, and then the front abdominal region, hanging head downwards (Fig. 28 *a*) until the cuticle of the




*c.*

FIG. 28.

*a*, *b*, *c*, Stages in emergence of Dragon-fly (*Aeschna cyanea*) from its nymph-cuticle. Natural size. From Latter, "Nat. Hist. of Common Animals".

legs becomes hard and firm. Then vigorously bending forwards, it catches hold, with its feet, of the front part of the empty nymph-cuticle (*b*) or the plant-shoot above it, withdraws the rest of the abdomen, and waits for the cuticle of that region as well as the wings to expand, dry, and harden, much as already described for the emerging grasshopper (Fig. 28 *c*). For some time after it has acquired the power of flying the dragon-fly has not yet assumed the deep colours and developed pattern that characterize its species ; such a relatively newly-emerged insect is defined as *teneral*.

Comparing generally the dragon-fly's life-story with the grasshopper's, we notice such a divergence between parent and young that the latter affords a fair example of a *larva*, in which the true relationship is masked, and we realize that this divergence is emphasized by the larva's aquatic mode of life involving special temporary breathing organs often of much complexity. The life-history may therefore be included among insect transformations. But the dragon-fly resembles the grasshopper in being active through all the larval and nymphal stages, and in displaying visible external wing-rudiments at an early period of its life.

With the life-histories of the grasshopper and the dragon-fly we may now compare that of a butterfly or moth,[1] which affords, perhaps, the most familiar example of all insect transformations. First of all it will be necessary to consider the structure of the perfect winged insect, so that the contrast between this and the larva or caterpillar may be rightly appreciated. A typical butterfly or moth is a more specialized insect than a grasshopper, more delicate in build, more perfectly adapted as a flying organism. In general plan of body there is, of course, agreement : the head with its conspicuous feelers, the thorax with its six legs and four wings, the ten-segmented abdomen ; but in points of detail there are some marked divergences. The scaly covering of almost the whole insect, the scales being flattened cuticular elements of the nature of hairs, is a highly characteristic feature.

The butterfly's head (Fig. 31 A), has large sub-globular

[1] G. Rolleston and W. Hatchett Jackson: "Forms of Animal Life". Oxford, 1888.

compound eyes (*e*) like the dragon-fly's, though not relatively so extensive or prominent. The feelers are many-jointed, showing in butterflies the extremity thickened like a club, bearing in many moths a wealth of sensory bristles, these being

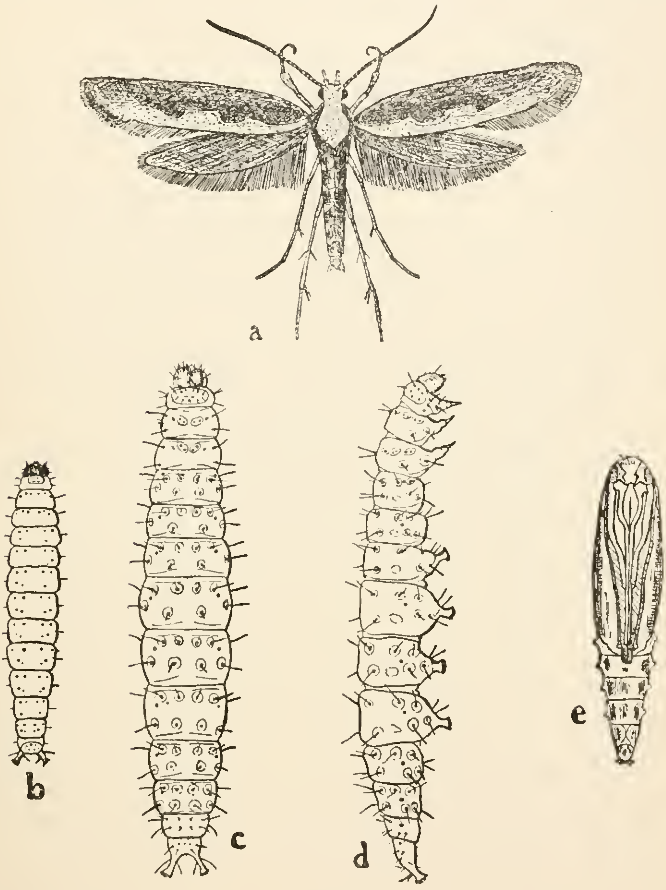



FIG. 29.
*a*, Diamond-back Moth (*Plutella maculipennis*) *b*, young caterpillar, dorsal view; *c* full-grown caterpillar, dorsal view; *d*, side view; *e*, pupa, ventral view. × 6. From Carpenter, " Life Story of Insects ".

in some cases borne on stiff or delicate outgrowths of the segments of the feeler, which thus assumes the appearance of a beautifully moulded comb or feather. But the most striking specializations of the butterfly's head-appendages are seen in

the jaws. Unless they be possibly represented by a pair of tiny pointed lobes (Fig. 31 A, *m*) attached to the upper lip, mandibles are altogether wanting. The *maxillae,* on the other hand, are most highly specialized for sucking liquid food, their outer lobes (or *galeae*) (Fig. 31 A, *g*) being drawn out into long flexible structures, grooved on their inner faces so that when applied to one another and fastened by a suitably arranged set of interlocking bristles, they form a tubular trunk which can be stretched out so as to gather nectar from plant-blossoms, or coiled up—somewhat in the manner of a watch spring—beneath the head. On the outer edge of the base (Fig. 31 B *b*) whence this galea springs is borne a palp (*p*), which in butterflies and the vast majority of moths is a mere vestige—a slender process with a terminal knob and a tuft of scales—but which in some families of small moths is developed in the typical jointed form. No trace of the inner maxillary lobe (*lacinia*) can be detected except in a single family of very small insects which stand at a markedly lower stage of specialization than typical moths and butterflies. The labium is also highly modified, with the suppression of some of its parts ; it consists of a transverse narrow plate beneath the maxillae, bearing a pair of rather conspicuous, upturned, scaly palps (Fig. 31 A, *p*), but with the typical paired lobes (*galeae* and *laciniae*) represented only by a small median process.

The butterfly's thorax is more compact that the grass-hopper's with the segmentation less evident. The prothorax is less prominent ; being covered with scales its form is not readily appreciated by cursory observation, but a pair of erectile scaled plates (the *patagia*) on the dorsal aspect are noteworthy. The mesothorax has also a pair of dorsal scaled plates (the *tegulae*), which overlie the bases of the forewings. The wings, with their usually close clothing of scales, arranged often so as to produce a coloured pattern of brilliance and beauty, are a dominating feature of the insect. The forewing is longer than wide, sub-triangular in shape, and relatively stiff in texture, while the hindwing, shorter and usually broader, may have the region occupied by the anal nervures capable of slight folding. The nervuration (Fig. 35) is predominantly longitudinal, the cross-nervules so abundant on the wing of

grasshopper and dragon-fly being very few. The butterfly's legs are comparatively slender, largely covered with scales, and armed with spines. Each foot has five segments, and it seems that in this number the butterfly shows a more primitive character than is found in the grasshopper or the dragon-fly with its three-segmented foot. But there are some butterflies

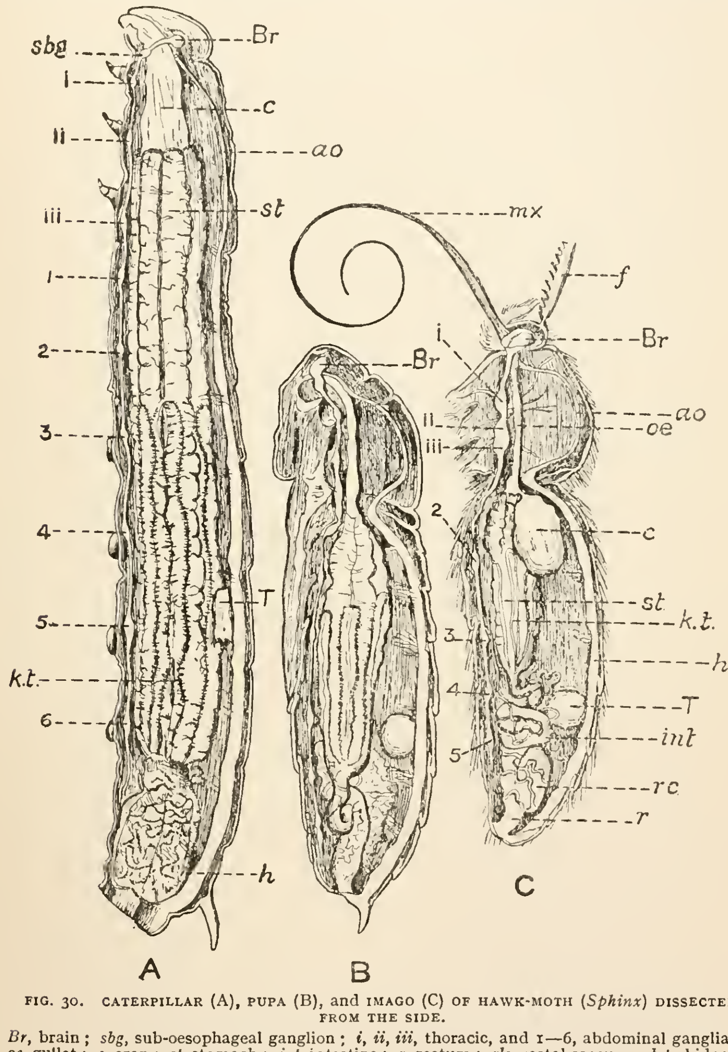



FIG. 30. CATERPILLAR (A), PUPA (B), and IMAGO (C) OF HAWK-MOTH (*Sphinx*) DISSECTED FROM THE SIDE.

*Br*, brain; *sbg*, sub-oesophageal ganglion; *i*, *ii*, *iii*, thoracic, and 1—6, abdominal ganglia; *oe*, gullet; *c*, crop; *st*, stomach; *int*, intestine; *r*, rectum; *rlc*, rectal caecum; *k.t.*, kidney tubes; *h*, heart; *ao*, aorta; *T*, testis. After Newport, *Phil. Trans. R.S.*, 1834.

in which the legs of the front pair are greatly reduced, the short shins clothed with delicate scales giving the appearance of fine brushes, and the feet being suppressed.

The internal organs (Fig. 30 C) of the butterfly or moth also display some important modifications. As the jaws are adapted for taking liquid and not solid food, the gullet in the head-region is expanded to form a sub-globular sac, whose walls, capable of contraction and dilatation through the action of appropriate muscles, serve to suck in the fluid nourishment through the trunk. Further, the crop instead of being placed directly between gullet and stomach is a blind, bladder-like side-outgrowth (Fig. 30 C *c*) of the former and a somewhat similar blind outgrowth of the hind-gut forms a rectal cæcum (*r c*). As no solid food is swallowed there is no gizzard, mastication and straining of particles not being required. The excretory tubes, very numerous in the grasshopper, are only four in number in the butterfly.

In the central nervous system a noteworthy specialization is seen in the close approximation of the second and third thoracic ganglia which appear to form a single large nerve-centre (Fig. 30 C, ii, iii) situated in the mesothorax, and the prothoracic ganglion (i) lies immediately in front. Such a marked centralization of portions of the ventral nerve-cord is carried to a still further stage in other highly-organized insects. The chain of abdominal ganglia retains in the moth or butterfly much the same extended arrangement that it has in the grasshopper, but here also there is often condensation, only four or five distinct centres being recognizable (Fig. 30 C).

From the egg, laid by the female butterfly or moth on a leaf of some suitable food-plant, is hatched the characteristic larva familiar as a *caterpillar* (Fig. 29 *b c d*). The caterpillar has a worm-like cylindrical body, most of the area of the cuticle being thin and flexible, so that the creature is comparatively soft, though on each segment there is a regular series of bristle-bearing tubercles, and when the bristles are very strongly developed, the caterpillar becomes markedly spiny or hairy.

The head-capsule (Fig. 31 C) is hard and firm, the cuticle being thick and compact, and a comparison of the caterpillar's head with that of the adult insect is instructive. In place of the butterfly's large compound eyes, the caterpillar has a

group of three or four simple eyes (*ocelli*) on either side, while the feeler (*At*) is short, consisting of only three segments each nearly as broad as long. A most striking divergence from the adult shown by the larva, is the presence of a pair of strong biting mandibles (*Mn*), essentially like those of a grasshopper or dragon-fly, for the caterpillar, unlike its parents, swallows solid food consisting of leaves or other plant-tissues which it bites off and devours. The maxillae (*Mx*) are curiously simple, each consisting of a two-segmented base which

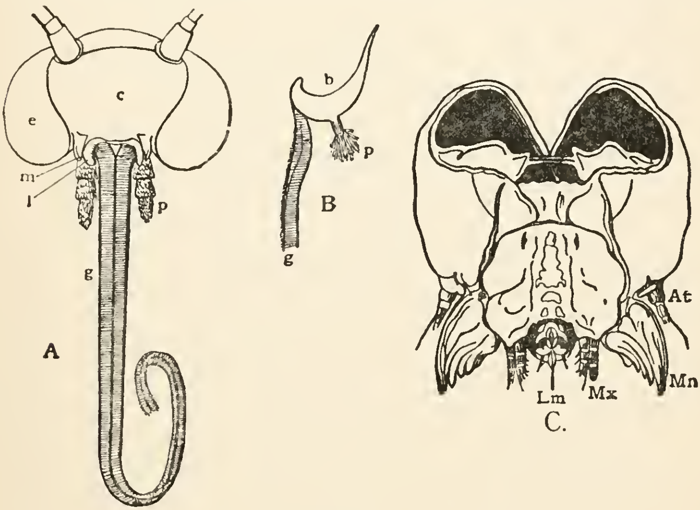



FIG. 31.

A, Head of a Moth, showing sucking trunk formed by flexible maxillary galeae (*g*) between labial palps (*p*); *c*, face; *e*, eye; *l*, labrum; *m*, doubtful vestigial mandible. B, Basal part of maxilla (*b*) removed from head; *p*, vestigial palp. Magnified. C, Head of goat-moth Caterpillar (*Cossus*) seen from behind; *At*, feeler; *Mn*, mandible; *Mx*, maxilla; *Lm*, labium with spinneret projecting beyond it. From Carpenter, "Life Story of Insects" (C. after Lyonet).

carries a short bristle-bearing palp and outer and inner lobes, corresponding apparently to the typical galea and lacinia. Between the maxillae is situated the labium (*Lm*), which has a large basal plate (*mentum*) bearing a pair of small palps. Just in front of the labium within the mouth is a conical chitinous process usually regarded as an outgrowth of the tongue (*hypopharynx*). This is the caterpillar's spinneret (Fig. 32), for at its tip there opens the duct leading from the silk-glands—most important and characteristic larval organs, as they produce a sticky fluid which, hardening on exposure to the

air, forms silken thread of great value to many caterpillars in their various life-activities, being used for the construction of protective webs on which some larvae live, and more frequently for cocoons or supports during the pupal or resting stage. Small spiny lobes on the front aspect of the tongue in various caterpillars have been detected[1] and identified with maxillulae.

Behind the head come the three segments of the thorax, each with a pair of jointed chitinous legs, short indeed when compared with those of the butterfly or moth, but with the haunch, thigh, and shin regions fully recognizable, while the unsegmented foot carries a single claw. The caterpillar's prothorax is often protected dorsally by a strongly chitinized plate, the presence of which distinguishes that segment. A spiracle is conspicuous on either side of the prothorax, but it is noteworthy that these air-openings are not present on the mesothorax and metathorax, the segments which in the adult bear the wings.

The caterpillar's abdomen is elongate, being made up of ten distinguishable segments, of which the first, second, seventh, eighth and ninth are always limbless, while the third, fourth, fifth, sixth, and tenth usually carry each a pair of short, stout, cylindrical appendages known as *prolegs*. These are unjointed, covered with thin, flexible cuticle like that of the caterpillar's body generally, and provided at the extremity with rows of short spines arranged either in a circle around the circumference of the prolegs, or in a crescentic ridge along its inner edge. The effect of this distribution of limbs in the caterpillar is to afford support at either end of the body—by means of the thoracic legs in front and the tail-prolegs or "claspers" (those on the tenth abdominal segment) behind, and also in the middle region of the body by means of the prolegs on the third to the sixth abdominal segments inclusive. Such a provision for support is clearly advantageous to a worm-like creature that has to crawl along a twig or to balance itself on the edge of a leaf, eating as it goes. In many caterpillars, modification of the typical arrangement of prolegs here described is to be found, notably through a reduction in the number of pairs of these limbs which necessitates a modification in the method of locomotion. On each of the first eight

[1] J. J. De Gryse: "The Hypopharynx of Lepidopterous Larvae," *Proc. Entom. Soc. Washington*, XVII. 1915.

abdominal segments there is a pair of laterally-situated spiracles so that—including the prothoracic spiracles already mentioned —the caterpillar has nine of these air-openings along either side of its body (Fig. 29 *d.*)

Turning now to the internal organs of the caterpillar, some remarkable and suggestive contrasts to the corresponding structures in the butterfly may be noticed (Fig. 30 A). The

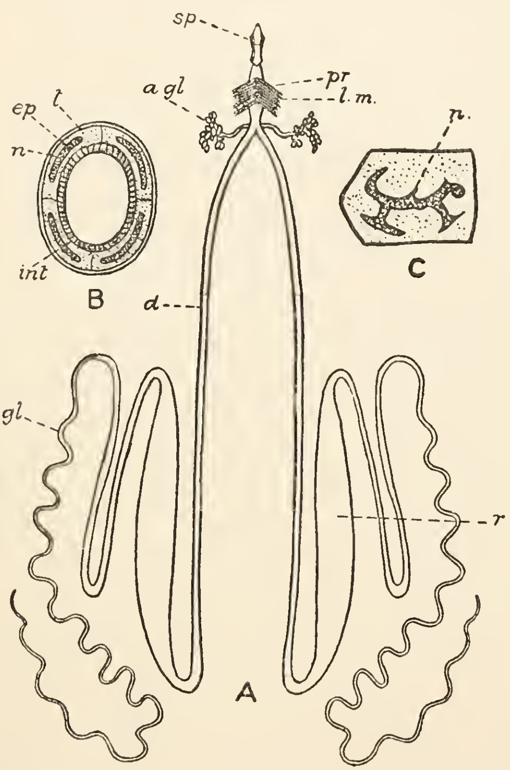



FIG. 32.

A, Diagram of a Caterpillar's Silk-glands (*gl*) with their reservoirs (*r*), ducts (*d*), and accessory glands (*a, gl*) ; *pr*, silk press ; *l.m*, its lateral muscles ; *sp*, spinneret. Magnified. B, Silk-gland in cross-section ; *ep*, epithelium ; *t*, tunic ; *int*. chitinous lining. C, A cell of the glandular epithelium in surface view with its branched nucleus (*n*). Highly magnified. In part after Helm, *Zeitsch. f. Wiss., Zool.* XXVI.

*food-canal* runs straight through the body from mouth to anus, and while the fore-gut (*gullet* and *crop*) and the hind-gut (*intestine* and *rectum*) are relatively small, the mid-gut (*stomach,*

Fig. 30 *st*) is long and voluminous, often with sacculated walls, providing an extensive area where the digestion of the abundant vegetable food-stuff which the caterpillar swallows, and the subsequent absorption of the extracted food-products can be adequately carried on. The paired silk-glands, to which reference has already been made, are long tubular organs (Fig. 32 A)—apparently modified salivary or spittle-glands—which lie in the great blood-space on either side of the food-canal, folded or twisted in their course as their length, if extended, would exceed that of the body. The ducts of these silk-glands unite to form the median duct or tube which opens, as already mentioned, at the extremity of the spinneret (Fig. 32 A) within the mouth. The cells (Fig. 32 C) which make up the walls of the silk-glands, whose function is to secrete the sticky fluid, obtaining the necessary material from the surrounding blood, are remarkable on account of their large, complex nuclei, each of which projects by a series of lobate processes into the surrounding protoplasm of the cell. The terminal region of the silk-duct, immediately before its opening through the spinneret is surrounded by a thick elastic chitinous wall forming the " press " by means of which the secretion of the glands is forced out in the form of a prismatic or flattened ribbon which solidifies to form the insect's silken thread, the pressure on the emerging silk being regulated by the action of suitably arranged muscles attached to the " press " (Fig. 32 A *pr*).

In the caterpillar's nervous system, it is of importance to notice the three distinct and separated thoracic ganglia (Fig. 30 A, i, ii, iii) and the chain of six or seven abdominal ganglia (1–6). It is evident that the concentration of the nervous system, so marked a feature in the structure of the butterfly, is not effected in the larva. The reproductive organs—ovaries in the female or testes in the male—have had their origin during embryonic growth, and are recognizable beneath the caterpillar's dorsal abdominal wall (Fig. 30 A, *T*).

In the life-period of the caterpillar, whose structure has now been briefly reviewed, there is a feature that, though very familiar, calls for especial emphasis. The description that has just been given would fit most caterpillars at any period of their lives. During the first stage, when the little larva

has been newly hatched from the egg, the main features both outward and inward, are all present and recognizable. The insect begins to feed voraciously, grows fast, and has to moult four or five times during larval life. While some of these moults may be followed by changes in detail with regard to the arrangement of hairs or spines, or to the colour of the

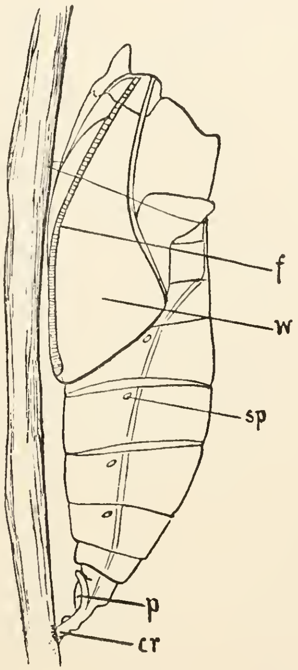



FIG. 33.

FIG. 33. PUPA OF WHITE BUTTERFLY (*Pieris*), SIDE VIEW. *f*. feeler; *w*, wing; *sp*, spiracle; *p*, anal proleg; *cr*, cremaster. ×8. From Carpenter's "Life Story of Insects," in part after Hatchett Jackson, *Trans. Linn. Soc.*, 1890, and Tutt, "Brit. Butterflies".

cuticle in certain regions, there is no change in the general aspect of the caterpillar despite its great increase in bulk, and at no time during larval life can any trace of outward wing-rudiments like those of the grasshopper and dragon-fly nymph be seen on the second and third thoracic segments which are destined to bear the wings in the imago.

As is well known, a great and apparently sudden change is

evident after the caterpillar has moulted for the last time. In preparation for this process of *pupation*, the insect spins a quantity of silk, greater if, as in the case of many moths a complete cocoon is provided for the covering of the body, less if, as with most butterflies, a pad for the suspension of the

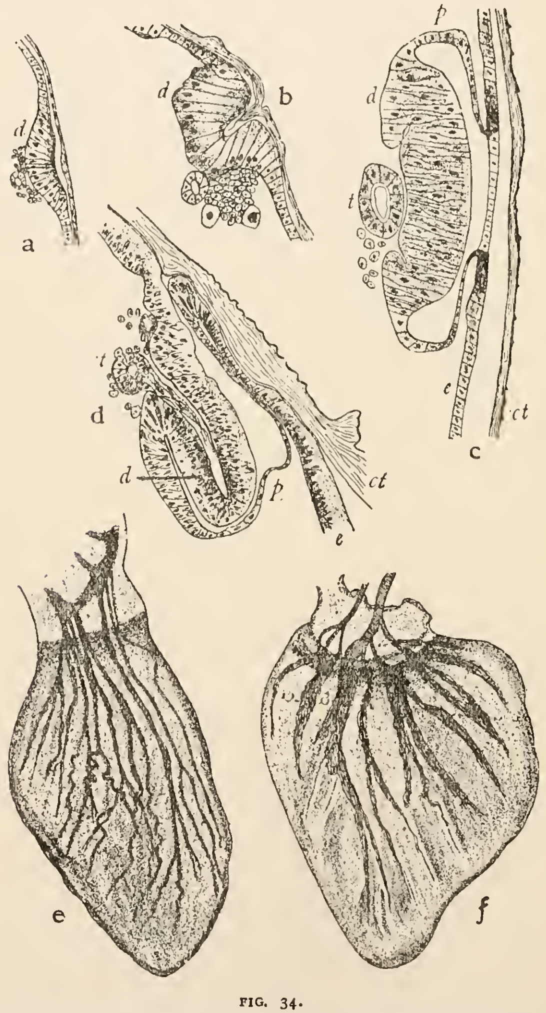



FIG. 34.

*a*, *b*, *c*, *d*, Sections showing successive stages in the development of the wing-bud of Butterfly (*Pieris*); *e*, skin; *ct*, cuticle; *d*, wing-bud; *p*, pouch; *t*, air tubes. × 100. *e*, *f*, surface views of buds, fore- and hind-wings in last larval stage, showing tracheation. × 12. From Comstock after Mercer, *Journ. N.Y. Ent. Soc.* VIII.

pupa by the tail is alone required. Spinning concluded, the body of the caterpillar becomes much shortened and the larval cuticle, splitting lengthwise in the mid-dorsal line, is slowly worked off the body from before backwards. Thus the form of the pupa (Figs. 29 *e*, 30 B, 33) is revealed, and examination shows that it prefigures all the characteristic structures of the butterfly. Wing-rudiments (Fig. 33 *w*, 35) of the same subtriangular shape as the butterfly's forewings, although smaller, lie on either side of the body ; on each side of the head is the area of the compound eye ; the mandibles, so prominent and important in the caterpillar, have disappeared, but the long, jointed maxillary galeae which make up the sucking trunk of the imago, lie side by side stretching backwards from the head beneath the ventral region of the thorax between the feelers (Fig. 33 *f*) and the fully-segmented legs which are packed between the costal edges of the wing-rudiments. The abdomen—covered like the rest of the pupa by a cuticle which soon becomes firm and largely rigid—is much shorter than the same region in the caterpillar ; its segmentation is well-marked, and the presence of flexible cuticle at three or more of the intersegmental junctions allows a restricted degree of movement. The tail-end is pointed, the spinose extremity (or *cremaster*) (Fig. 33, *cr*) serving to anchor the pupa to its cocoon or its suspensory pad.

Consideration of the apparently sudden production of these organs at the pupal stage suggests some important questions. Have they indeed been then formed for the first time, and if not, why is no trace of them to be seen through all the changes of the caterpillar-life ? The answer leads us to appreciate the inwardness of the butterfly's type of life-history. Thinking especially of the wing-rudiments, so conspicuous externally on the nymphal grasshopper or dragon-fly, we dissect a half-grown caterpillar and find within the second and third thoracic segments little flattened pads (Fig. 34 *e f*), into which air-tubes run, lying in pouches connected with the body-wall.[1] These are the wing-rudiments, yet though dissection is needed to demonstrate their existence, they are not, properly speaking, internal organs. Study of a series of sections shows that they

[1] J. Gonin : " Récherches sur la Métamorphose des Lépidoptères ". *Bull. Soc. Vaud. Sci. Nat.*, XXXI. 1894.

arise as buds or thickenings of the outer body-wall (Fig. 34, *a*, *b*). These, by growth and inpushing of the adjacent skin, come to lie in pouches (Fig. 34, *c*, *d*), and as they do not project externally beyond the skin no cuticle is formed over them. Only towards the end of the last larval stages are they pushed out of their pouches, and then the new cuticle must of necessity clothe them so that in the pupal stage they will be outwardly visible. Further, it is found that the other characteristic structures of the butterfly first revealed in the pupa—the long feelers, maxillae and legs, for example—are similarly developed in the caterpillar from buds arising in inwardly-directed pouches. As all these are rudiments of structures in preparation for the perfect winged insect (or *imago*) they are known generally as *imaginal discs* or *imaginal buds*. Rapid growth of these takes place during the last larval stage, and as the body of the pupa is thus built up, many structures of the caterpillar are broken down, their cellular elements dissolved as they are no longer needed for the insect's life.

It is well known that the pupa of a butterfly takes no food and remains passive ; if stimulated, only a twitching of those few abdominal segments capable of movement on each other can be observed. The pupal stage marks a definite period of quiescence in the life-history, which is indeed essential because the divergence between the larva and imago necessitates such dissolution and reconstruction for which, as we have seen, provision is made by the destruction (*histolysis*) of much larval tissue and the formation of the perfected organs from the imaginal discs. This process is continued through the pupal stage, the cuticular structure of the butterfly —scales, hairs, spines—being formed beneath the pupal cuticle. The emergence of the imago from this cuticle is essentially like that of the developed grasshopper or dragon-fly. Through the dorsal, longitudinal slit, the head, thorax, wings, legs and abdomen are successively withdrawn ; the new cuticle then sets and hardens ; the wings, small and crumpled immediately after emergence, expand and stiffen ; and the aerial life, for which, as has been seen, preparation began long before in the hidden growth of the caterpillar's imaginal buds, is at length attained.

The life-history of the butterfly, compared with that of the

grasshopper or dragon-fly, shows a striking peculiarity in the resting, pupal stage and—so far as the former is concerned—in the unlikeness of the young insect to the parent. This unlikeness too is much more marked in the butterfly than in the dragon-fly; the caterpillar is truly a larva—a young creature whose parentage and destiny are alike masked by its appearance. Yet the divergence between butterfly and caterpillar must not be exaggerated; the fundamental struc-

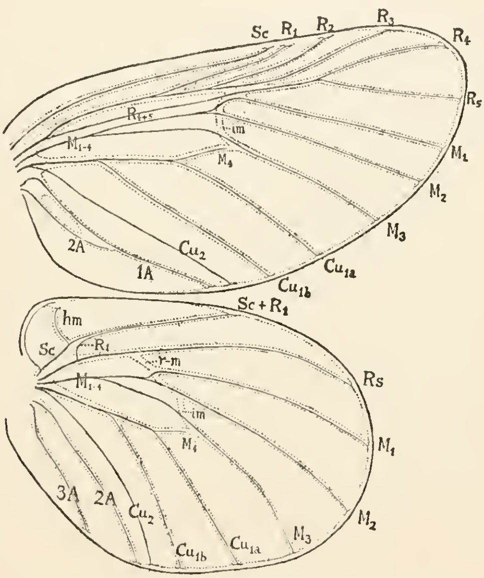



FIG. 35. WINGS OF A BUTTERFLY PUPA (*Euploea*)
Showing the system of tracheation, the incipient nervures indicated by dotted lines. *Sc*, sub-costal; *R*, radial; *M*, median; *Cu*, cubital; *A*, anal tracheae of nervures, the branches of each system numbered. About thrice natural size. After Tillyard, *Proc. Linn. Soc.*, *N.S.W.*, XLIV.

tures of the parent—even to wings and reproductive organs—are in the offspring, though in an undeveloped or degenerately modified form. Lastly we notice that, while in the growth of grasshopper and dragon-fly outward wing-rudiments appear at an early stage, these structures are in the caterpillar directed inwards, and thus they remain hidden until the formation of the pupa brings to pass the due time for their appearing.

The three insect life-histories, which it has been sought to sketch in sufficient detail for the appreciation of their salient features, illustrate therefore an increasing divergence in form between the adult and the young. In succeeding chapters many further examples of this most important aspect of insect transformations will be given ; it will be seen, for example, that the common flesh-eating maggot differs far more profoundly from its parent blue-bottle than the caterpillar differs from the butterfly, though its mode of growth is essentially of the same type. Such insects, whose wing-rudiments, hidden in the larva, appear outwardly only in the resting pupa, are often said to pass through a " complete transformation " and are defined as *holometabolous*, while the type of life-history exemplified by the dragon-fly has been defined as an " incomplete transformation ", insects conforming to it being distinguished as *hemimetabolous* ; the grasshopper which, after hatching, undergoes no conspicuous change except the acquisition of wings might be regarded as an *ametabolous* insect, or one with no feature in the life-history that can fairly be regarded as a " transformation ". Thus each of the three insects might be taken to represent a special section of the class to which they belong when studied from the standpoint of development. But it must be admitted that between the grasshopper and the dragon-fly—as between the butterfly and the blue-bottle—the developmental difference is one of degree, while between the grasshopper and the dragon-fly on the one hand and the butterfly and blue-bottle on the other, there is a distinction that seems fundamental. The two former have outward and visible wing-rudiments ; in the latter these structures grow so as to be concealed until the characteristic pupal stage is reached. This fundamental distinction has been emphasized in recent years[1] by laying stress on the contrast between the outward and the inward (*exopterygote* and *endopterygote*) or as they might perhaps be suitably termed the " open " and the " hidden " types of wing development, further examples of which will be discussed respectively in the next two chapters of this book.

[1] D. Sharp : " Some Points in the Classification of Insects ". *Fourth Internat. Zoolog. Congress*, 1898. Cambridge, 1899.

CHAPTER III

# THE OPEN TYPE OF WING-GROWTH

THE type of development seen in such life-histories as those of the grasshopper and the dragon-fly is characteristic of a large assemblage of insects which, differing widely among themselves in structure and habits, are distributed by systematic students into various orders. In the selection of illustrative facts which it is proposed now to give, some attempt will be made to set forth those modifications of the open type of wing-growth which seem most important for the understanding of insect transformation in its broad aspect. Many details, interesting in themselves, will find therefore no mention in this chapter.

Some account of the general build of an insect-wing has already been given in connexion with the brief survey of the structure of the adult grasshopper. It may be well now to return to this subject at the outset of our discussion on wing-growth, tracing the main steps in the development of the organ from the early wing-rudiment.[1] This begins as a hollow outgrowth from the junction of the dorsal and pleural regions of its thoracic segment, the columnar cells of the skin (*epidermis*) forming a sheet which encloses a prolongation of the great body blood-space of the young insect. The early wing-rudiment may be at first tubular in form, but it tends to become flattened through the approximation of its dorsal and ventral walls, the individual cells of the skin becoming spindle-shaped. Into this hollow rudiment grow air-tubes arising from the dorsal trunk of the larva ; in a typical wing-rudiment these tubes correspond with the main nervures of the developed wing already mentioned : costal, subcostal, radial, median, cubital and several anal (Fig. 35)—some of

[1] J. H. Comstock : " The Wings of Insects ". Ithaca, New York, 1918.

them giving off branches and penetrating further as the structure increases in size at each moult. These air-tubes convey the oxygen needed by the growing tissues and also prefigure the scheme of nervuration of the perfected wing, the main nervures following generally the tracks of the air-tubes, in some cases coming to enclose both them and fine nerve-cords which follow their courses, and being distinguished by the same names. The two layers of the wing-fold come into contact with each other except along the courses of the air-tubes to which the blood-spaces thus become restricted (Fig. 36). During the last larval or nymphal stage the wing-nervuration begins to form definitely beneath the cuticle soon to be cast off, the new cuticle showing thickenings along the courses of the air-tubes. As these are often situated alternately nearer


FIG. 36. SECTION THROUGH WING-RUDIMENT OF A NYMPHAL DRAGON-FLY (*Anax*).

Showing the two folds approximated except where traversed by the air-tubes; *ep*, skin (*epidermis*); *bm*, basement membrane; *c*, cuticle; *C*, costal; *A*, anal edge of wing. × 40. After Comstock and Needham, *Amer. Nat.* XXXIII.

to the upper and lower surfaces of the developing wing, the cuticular thickenings arise in correspondingly alternate positions resulting in the formation of *convex* nervures on the upper surface and *concave* ones on the lower aspect of the perfected wing. Reference has been already made in the preceding chapter (pp. 38, 64) to the manner in which the growing wings of the adult are folded within the cuticle of the wing-rudiments of the last nymph-stage (Fig. 37 *a b*). The process of unfolding and expansion has been carefully traced[1] in various species of termites (the so-called " white ants "). The growing wings (Fig. 37 *c d e*) are closely crumpled and rolled and their expansion works outwards from base to tip; " the process may well be likened to the billowing out of a crumpled and wet cloth by driving a blast of air below it ".

[1] Claude Fuller: " The Wing-Venation and Respiratory System of Certain South African Termites ". *Ann. Natal Mus.*, IV. 1919.

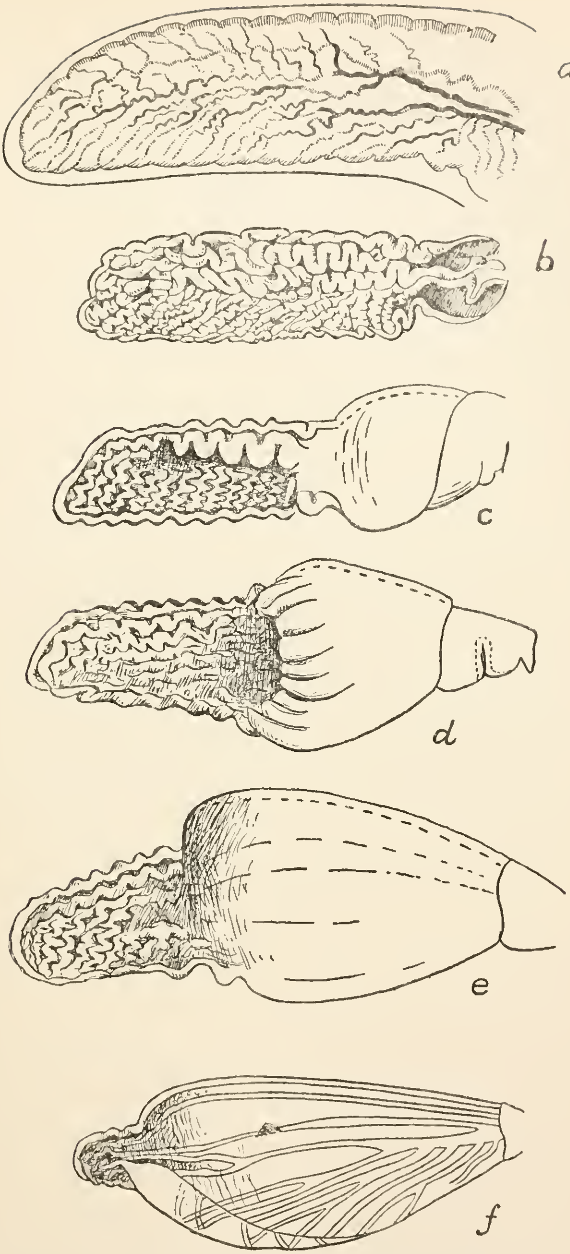



FIG. 37. DEVELOPMENT OF WING OF *Termes natalensis*.

*a*, nymphal wing-rudiment with crumpled imaginal wing inside; *b*, wing just after last moult; *c*, *d*, *e*, *f*, stages in unfolding of wing. × 10. After Fuller, *Ann. Natal Mus.* IV.

As after the final moult, the wings thus expand, the cuticle extends, thickens and hardens ; the skin-cells become flattened and, over the extensive areas of the wings where the two layers are in contact, they may degenerate and die, leaving the upper and lower sheets of cuticle coalesced into a stiff membrane supported by the thickened nervures which form what might be termed the skeleton of the wing (Fig. 37 *f*, 43 *a*).

A subject of much interest in connexion with wing-growth is afforded by the varying degree of development attained by the wings in insects of the same or of nearly allied kinds. In the great majority of grasshoppers, locusts and crickets—which all resemble the insect taken as an example in the previous chapter (pp. 5–28) in the elongate and strong hindlegs—wings capable of supporting the creature in flight are developed as already described. But not a few of these jumping insects attain the adult condition provided only with short wing-rudiments quite useless for flight, and in some there is no trace of wings at any stage. To the same order (Orthoptera) as grasshoppers and locusts, belong the familiar kitchen and shipboard cockroaches among which wings are developed in essentially the same way. In the common kitchen cockroach (*Blatta orientalis*)—the insect often erroneously termed a " black beetle "—the male (Fig. 38 *b*) has rather short but perfectly formed wings, while in the female (Fig. 38 *a c*) these organs never get beyond the condition of early rudiments. A similar sexual differentiation is to be noticed in many cockroaches inhabiting tropical countries, and some members of the family are without any wings at all. On the other hand the American cockroach (*Periplaneta americana*) of ships, quays, and hothouses, has very well developed wings in both sexes, and so has the small but prolific German cockroach (*Phyllodromia germanica*) of bakehouses. Such facts as these will be found very suggestive when, in a later chapter, the general question of winglessness among insects will come up for discussion.

There is another group of insects whose life-histories serve to elucidate this subject ; these are the Aphids—too well-known to gardeners as plant-lice or " greenfly ". They belong to an order (the Hemiptera) very distinct from that of the

grasshoppers and cockroaches, for their jaws are highly modified for piercing and sucking, so that they are adapted for taking not solid but liquid food. The labium is a long, jointed beak, projecting beneath the head ; on its front aspect is a groove within which the mandibles and maxillae, transformed into fine, needle-like piercers work to and fro. Thus the aphid, pressing the tip of its beak against the surface of a leaf, can perforate the plant-tissue with its piercing jaws

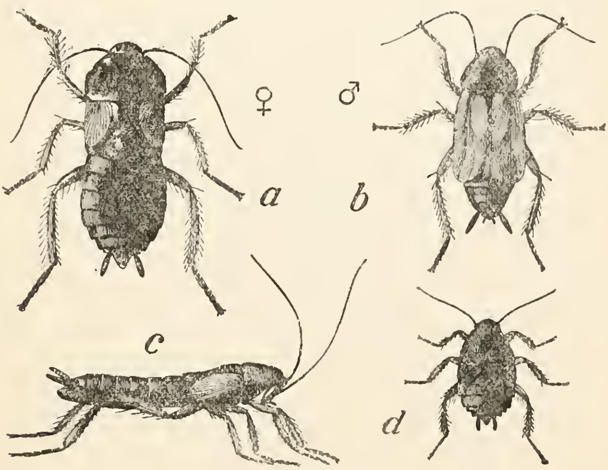



FIG. 38. COMMON COCKROACH (*Blatta orientalis*).
*a*, female ; *b*, male, dorsal views ; *c*, female, side view ; *d*, young with wing-rudiments. Natural size. From Carpenter, "Life Story of Insects," after Marlatt, *Entom. Bull.* 4, *U.S. Dept. Agric.*

and suck in a meal of sap through the narrow channel between them.

Most aphids pass the winter in the shelter of hard-shelled eggs laid on suitable plants during the previous autumn. From these eggs are hatched in the spring young insects (Fig. 39 *d*) which grow through a series of moults but with hardly any change of form into wingless females (Fig. 39 *c*) known as "stem-mothers". There are no males for these to mate with, and they have the power of producing young which, developing from unfertilized eggs within the mother's body, are born in an active state, and may themselves become adult

and capable of reproduction after less than two weeks' growth. Thus successive generations of females are rapidly produced during the spring by means of this curious virgin reproduction (*parthenogenesis*). Sooner or later a brood of young insects arise which, after a couple of moults, show narrow wing rudiments (Fig. 39 *b*) on the second and third thoracic segments; these grow into winged aphids (Fig. 39 *a*), the two wings of a side being alike delicate and gauzy in texture, the forewings much larger than the hindwings, both with a charac-

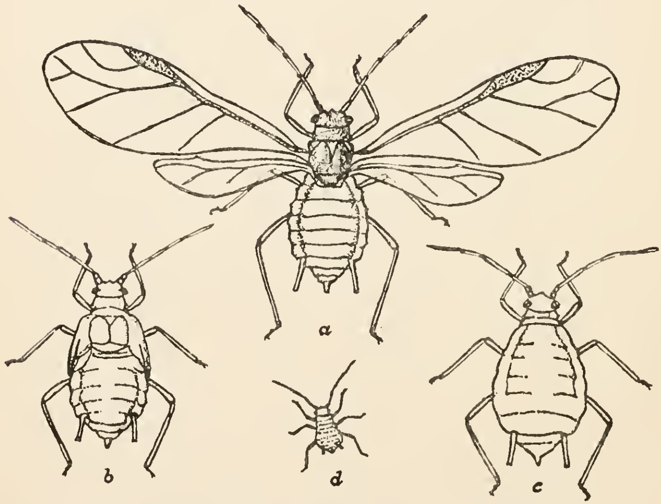



FIG. 39. VIRGIN FORMS OF GREEN APPLE APHID (*Aphis pomi*).
*a*, winged virgin female; *b*, its nymph with wing-rudiments; *c*, wingless virgin female; *d*, young. ×12. After Quaintance, *Entom. Circ.* 81, *U.S. Dept. Agric.*

teristically reduced nervuration, carried when at rest with the costa ventralwards. Such winged aphids can leave the plants on which they were born and migrate to others where there may be greater space and more abundant food. Thus through spring and summer the virgin generations succeed each other, some winged and some wingless, until with the approach of autumn, males and females are born which, after pairing, produce the hard-shelled winter eggs whence next spring's stem-mothers will be hatched. In different kinds of aphids

the autumn sexual insects may be all winged or all wingless, or the females may be wingless and the males winged (Fig. 40). The striking feature in the aphid life-cycle from our present standpoint is that a wingless mother gives birth to young that develop wings, and that the offspring of these may, in their turn, be wingless. A marked and sudden change of form is thus seen in the course of a single

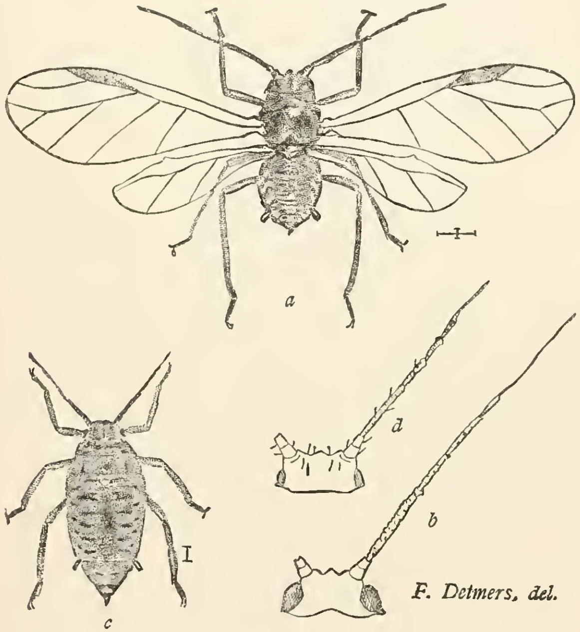



FIG. 40. SEXUAL FORMS OF CABBAGE APHID (*Aphis brassicae*).
*a*, male, × 15 ; *b*, head and feeler, × 30. ; *c*, female, × 12 ; *d*, head and feeler, × 30.
From Weed, "Insect Life", III.

generation. But occasionally intermediate forms with useless wings half the normal size or still more rudimentary, are produced.

The aphids may also serve to introduce another subject of much importance, one moreover that lends itself to extended treatment ; the varying amount of divergence between adult and young displayed by various insects that practise the open type of wing-growth. In the two examples described in the

preceding chapter it has been seen that there is very little divergence in the case of the grasshopper, and a somewhat wide difference in that of the dragon-fly. Between these two types a long series may be intercalated, while insects may be found in which there is a wider divergence between imago and larva than in the dragon-flies, and others in which the young differs from its parent less than a young grasshopper does. The aphids may fairly be claimed as examples of the latter. For while the newly-hatched grasshopper is distinguished from the adult by a characteristic relative shortening of the abdomen as compared with the thorax, the newly-hatched or newborn aphid is a closely approximate miniature of its parent, with which it agrees in the general form and proportions of its body.

Reference has already been made to the modification of the aphid's jaws for piercing and sucking, a character which it shares with all the members of its order. Other features of the head in these insects are the small but prominent compound eyes and the feelers (Fig. 40 *b d*) of six or seven segments, whereof the first and second are short and stout, while the others are elongate and slender, the cuticle provided with ring-like sense-organs ; the last segment of the feeler is suddenly constricted not far from its base, its terminal portion tapering and showing incomplete transverse furrows. In winged aphids the mesothorax and metathorax are relatively broader than in the wingless forms (Fig. 39 *a c*) and the tergal exoskeleton well developed, as is necessary to give attachment to the wing-muscles. In wingless forms, the thorax is hardly differentiated from the abdomen, and the cuticle is generally thin and soft all over the body. The abdomen is ovoid in shape, broadest at its third or fourth segment and tapering to the tail-end ; the sixth segment carries a pair of prominent outstanding tubes, the *cornicles*, organs most characteristic of the family, which pour out a sticky protective secretion. The legs of an aphid are relatively long, and feebly spiny, the foot consisting of two segments only.

In the newly-born young the general form and proportions of the adult are closely reproduced,[1] the legs and cornicles

[1] A. C. Baker and W. F. Turner : "Morphology and Biology of the Green Apple Aphis". *Journ. Agric. Research*, V. 1916.

showing their characteristic features, though they are relatively shorter than in the adult. The compound eyes have as yet but few facets, and there are only four segments in the feeler (Fig. 41 *a*), though the terminal one (the fourth) has the same distinctive form as the sixth in the adult. After the first

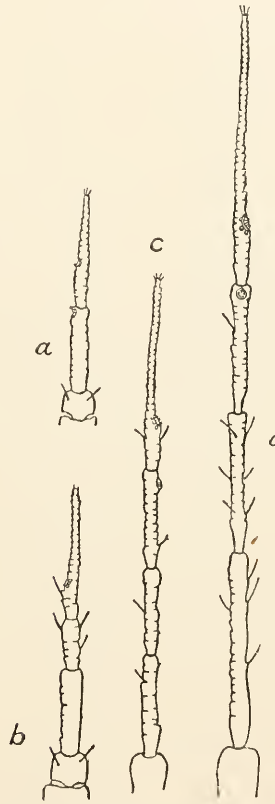



FIG. 41. FEELERS OF VARIOUS INSTARS OF A WINGLESS VIRGIN FEMALE OF *Aphis pomi*.

*a*, new-born; *b*, second; and *c*, third stages; *d*, adult. × 80. After Baker and Turner, *Journ. Agric. Res.* V.

moult the number of eye facets is increased and the feeler (Fig. 41 *b*) has five segments, a short penultimate one being, as it were, intercalated; and in the third stage (*c*) this region is divided into two, the full number (six) of the adult being thus attained. At the third stage also small wing-rudiments

appear on the second and third thoracic segments in those aphids that are destined to grow into winged insects, and after the next moult, when the fourth stage is reached, these are prominent, reaching backwards alongside the body as far as the third or fourth abdominal segment. After the fourth moult the adult condition is attained, and the winged aphids then display the hardened thoracic exoskeleton adapted for the attachment of the organs of flight. In the development of the wingless generations there is the same number of stages, but no trace of wing-rudiments, and the young naturally resembles the wingless more closely than the winged adult. The intermediate aphids, with reduced wings, already mentioned, are indistinguishable from their fully-winged sisters during the third and fourth stages, but, when adult, they resemble these less closely than they do the wingless forms, as the thoracic cuticle remains thin and the exoskeletal structures are unspecialized. The occasional development of these intermediate aphids may give a hint of the process whereby the wingless have become modified out of the winged forms among these insects. In the one case the wings attain but a feeble growth ; in the other they entirely fail to appear.

The young aphids not only resemble their parents closely in form, but live in similar surroundings and conditions. We may turn next to a group of insects in which while the young is generally like its parent, it lives in very different surroundings —in water instead of in the atmosphere. These insects are the Stone-flies, a small order (Plecoptera) allied to that of the cockroaches and grasshoppers (Orthoptera), for one of our larger species of *Perla* has biting jaws, often much reduced, wings of which the front pair are elongate and narrow and the hinder pair broad with an extensive folding anal area, though the forewing is (unlike that of a grasshopper or cockroach) of the same texture as the hindwing, and long paired cerci at the tail-end of the body. The head is relatively broad with a pair of long, many-jointed feelers, and the body generally is somewhat flattened from above downwards. These insects are found on the banks of streams or on half-submerged stones, sometimes flying rather heavily for short distances. The female drops her eggs into the water in which the young live. The young Perla has the broad head with long feelers and

compound eyes, the flattened abdomen with elongate tail-appendages that characterize the adult ; by means of its strong mandibles it catches and bites up small insects which serve it as prey. Living under water it needs some special adaptation for breathing, and this is found in six pairs of tufted tubular gills, situated on the sides of the thorax close to the bases of the legs and at the junction of adjacent segments. These gills are connected with the trunks of the air-tube system. Thus through a series of moults the young grows on towards its goal, showing outward wing-rudiments at an early stage, and finally crawling out of the water so that it may cling to a stone and allow the fly to emerge into the air where it can expand and dry its wings. With the development of these there is—as among the winged aphids—an elaboration of the second and third thoracic segments. The fly's jaws are weak compared with those of its aquatic young, as it lives but a short time and takes but little food. An interesting survival from the early life under water is seen in the presence on some stone-flies of the tufted tracheal gills in a withered and reduced state.

Some of the stone-flies also resemble aphids as well as cockroaches in a curious and interesting diversity in the size of the wings. In several species it is quite usual to find individuals with wings less than half the normal size, and this tendency to shortening is carried farther among males than among females—a sexual modification uncommon among insects, and opposite to that shown by the aphids and cockroaches in which abbreviation or disappearance of the wings is more often a female than a male character.

The great order of sucking-insects to which aphids belong comprises other families in which the young throughout their period of growth, display a striking likeness to their parents. We may take for example, a family of plant-bugs (*Capsidae*) which, like the aphids, feed by sucking sap from plant-tissues, some of them causing at times serious damage to foliage and young fruits in garden and orchard. An adult capsid plant-bug (Fig. 42 *g*) has a broad, bluntly triangular head with laterally-situated compound eyes and feelers which, although elongate, consist of only four segments, the basal one being stout and the other three long and slender Below the head is the

modified labium or beak, enclosing the piercing mandibles and maxillae, as already described for the aphids ; this beak, when not in use, extends backwards between the bases of the legs, its tip reaching the middle of the abdomen. The prothorax is broad and collar-like, wider behind than in front with prominent "shoulders", covering the front region (*scutum*) of the mesothorax, of which the triangular scutellum with apex directed backwards is the most conspicuous feature. The forewings borne on this segment have, in bugs generally the tip membranous and the basal two-thirds of firm texture, this latter region being divided into a costal and central area (the *corium*), and a dorsal area (the *clavus*) marked out by a straight suture ; in the capsid bugs, a small but distinct third area (the *cuneus*), is found between corium and membrane. The forewings, so largely firm and rigid, serve as protective coverings for the membranous hindwings (attached to the metathorax), which lie beneath them when not in use for flight. In this resting position the clavus of each forewing lies close against the scutellum, and the wings lying flat over the abdomen hide completely that region of the body. The legs are relatively long and slender, with three segments to each foot. Beneath the tip of the female's abdomen, in a narrow groove, lies the ovipositor ; this consists of blade-like processes by means of which the insect can lay her eggs (Fig. 42 *a*) partly imbedded in soft plant-tissues.

The newly-hatched young of a capsid bug is in most respects a miniature of its parent. In a species of *Plesiocoris* (Fig. 42 *g*) of which the life-history has been traced in some detail[1] it is a minute green insect about a millimetre ($\frac{1}{25}$ inch) in length with feelers having the same segmentation as in the adult, but relatively thicker, and the head being more acutely triangular. The three segments of the thorax are undifferentiated, and there is no trace of wing-rudiments ; each foot has as yet only two segments (Fig. 42 *b*). After its first moult, the little bug (Fig. 42 *c*) becomes 1·5 mm. in length ; in the next stage (Fig. 42 *d*) the corners of the mesothorax and metathorax are produced into blunt rounded lobes, the first indication of wing-rudiments. In its fourth stage the young

[1] F. R. Petherbridge and M. A. Husain : "A Study of the Capsid Bugs found on Apple Trees". *Ann. Appl. Biol.*, Vol. IV., 1918.

insect (Fig. 42 *e*) has attained a length of 2 mm.; its feelers have become relatively longer and more slender, and the wing-

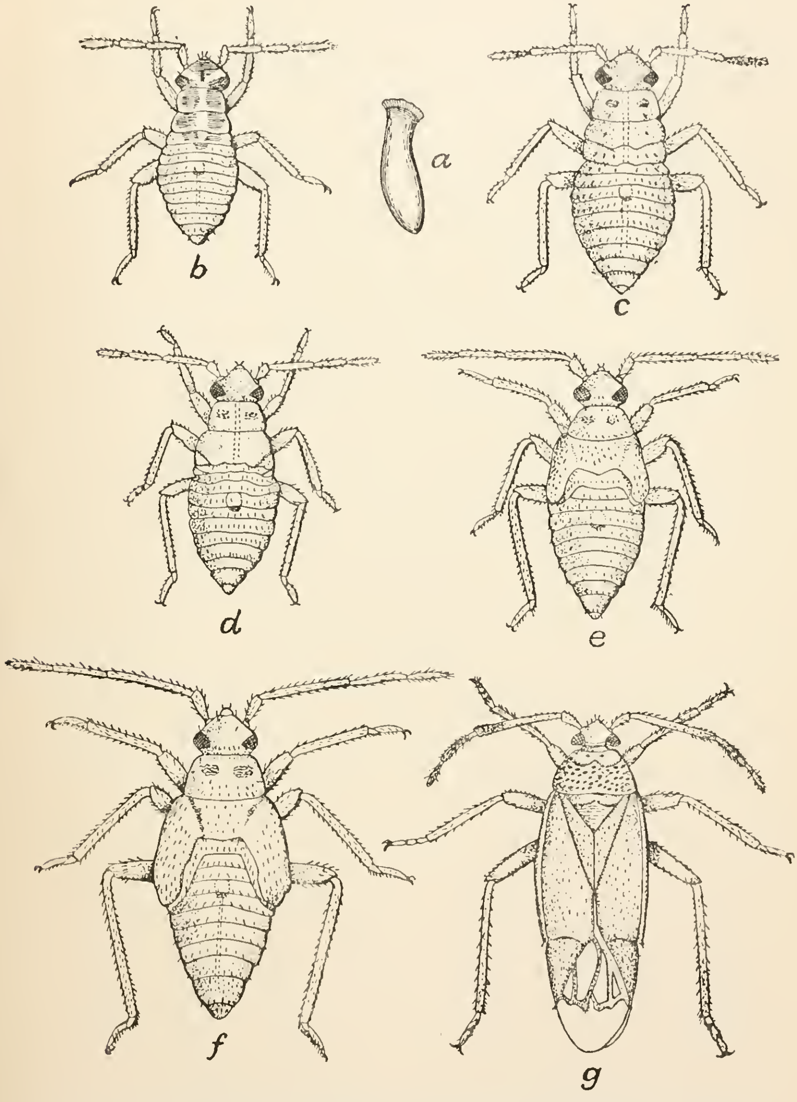



FIG. 42. STAGES IN THE DEVELOPMENT OF A CAPSID PLANT-BUG (*Plesiocoris rugicollis*).

*a*, egg; *b*—*e*, first, second, third and fourth instars (wing-rudiments minute in *d*, larger in *e*); *f*, last nymphal stage. × 20. *g*, adult. × 8. After Petherbridge and Husain, *Ann. Appl. Biol.* IV.

rudiments, now quite prominent, reach back to the second segment of the abdomen. The fifth-stage nymph (Fig. 42 *f*), is half as long again as the third, with the mesothorax largely increased in size, the wing-rudiments, which reach back to the fifth abdominal segment, showing the courses of the air-tubes that prefigure the nervuration of the developed imago. In the nymph stages of the bug, unlike those of the grasshopper or dragon-fly, the wing-rudiments lie almost flat on the back, the front pair mostly concealing the hind pair as they do in the adult. After the fifth moult the insect reaches the adult state (Fig. 42 *g*), in which its length is from 5 to 6 mm., so that through the stages of its life-history it grows about six-fold in length, and more than two-hundredfold in bulk. The period of growth from the newly-hatched young to the perfect, winged bug may be reckoned as about four weeks under favourable conditions.

We may now turn to consider some points in the development of a group of insects—the Termites or "White-ants"—which are of great interest on account of the varied forms which different members of the same species assume when fully grown and the complex social life of their families or communities which often become excessively populous. Details of the habits of termites do not come within the scope of our present subject; it is possible to consider only those features of their form and development which illustrate the methods of external wing-growth.

Termites[1] are insects with biting jaws like those of grass-hoppers or cockroaches, and slender, many-jointed feelers on the head. The wings, when fully developed, are very long in proportion to the size of the insect, those of the two pairs closely alike, with an excessive reduction of the anal area, with the typical series of longitudinal nervures, and with a network of cross nervules. At the tail-end are a pair of short jointed limbs (*cerci*) and (in males) a pair of ventral stylets, recalling the arrangement in cockroaches, to which the termites are believed by some students to be somewhat closely related,

[1] *See* B. Grassi and A. Sandias: "Constitution and Development of the Society of Termites". *Quart. Journ. Microsc. Soc.*, Vols. XXXIX, XL. 1897-8. K. Escherich: "Die Termiten oder weissen Ameisen". Leipzig, 1909. A. D. Imms: "Structure and Biology of Archotermopsis". *Phil. Trans. R. Soc.* (B), Vol. CCIX. 1919.

in spite of the similarity between their fore- and hindwings which leads others to place them in a distinct order (Isoptera).

A young termite, hatched from an egg laid by the " queen " or fertile female of the community, is strikingly like the winged adult in its general body-form, but is broader proportionally to its length. The head is widest at its hinder region and tapers slightly towards the front where the feelers, with fewer segments than in the adult, are inserted. The young termite (Fig. 43 *b*) is blind, though small compound eyes are present in the winged adult. The prothorax is constantly broader than long, but the other two thoracic segments, relatively elongate in the adult, are short in the young. After several moults, wing-rudiments (Fig. 43 *f*) can be distinguished on the mesothorax and metathorax, and the wings become, as usual, fully developed after the final moult (pp. 68–9). Winged termites are often found in great swarms in the tropical and sub-tropical regions which they inhabit, and the majority of such insects seem to fall a prey to birds. But those which survive and pair become the parents (" kings" and " queens ") of new family-societies ; spending their lives in a closed nest-chamber, they no longer require wings and these organs are shed after the nuptial flight, a transverse suture across the wing-bases rendering their loss easy (Fig. 43 *a*).

The chief interest afforded by termites to the nature-student, is found perhaps in the enormous numbers of wingless members of the societies which carry on the wonderful communistic activities of the nest. These, all developed from closely similar undifferentiated young, mostly belong to two well-marked types : the *worker* (Fig. 43 *c*) and the *soldier* (Fig. 43 *d*). The worker is usually a small, blind, wingless insect not markedly differing from the young form out of which it develops. The soldier has an abnormally large head, with very strong prominent mandibles ; members of this caste are usually blind like the workers, but in some cases feeble eyes are present. Workers or soldiers may belong to either sex ; usually their reproductive organs remain in a rudimentary state, but occasionally these become developed, this being apparently a common condition among soldiers of the primitive *Archotermopsis,* in which the accessory sexual characters may also be apparent. And it is of especial interest to find that

among workers, soldiers, and the preliminary stages through which they develop, vestigial wing-rudiments (Fig. 44 *a*) can in some cases be detected. In many termite communities

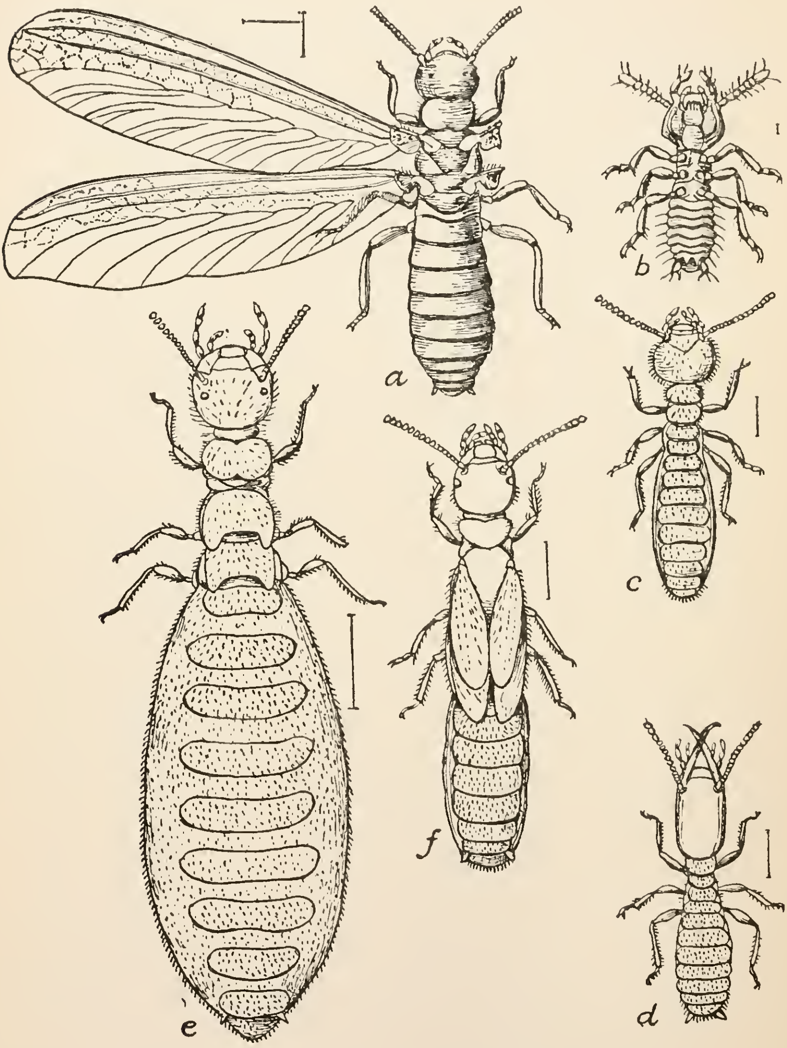



FIG. 43. FORMS OF NORTH AMERICAN TERMITE (*Calotermes flavipes*).
*a*, male (right wings truncated); *b*, larva (ventral view); *c*, worker; *d*, soldier; *e*, female ("queen"); *f*, nymph with wing rudiments. Magnified (the line alongside each figure shows natural size). After Marlatt, *Entom. Bull.* 4, *U.S. Dept. Agric*

individuals with developed reproductive systems, but with wings always in a rudimentary state, known as complementary or substitution "royalties", are kept in case of accident to the true royal pair. Thus the termites afford examples of various stages in the arrest of the normal development of wings on to the total disappearance of those organs.

In several groups of termites it has been noticed that after the last moult but one, the nymph spends some time—varying from an hour to three days—in a quiescent state, motionless

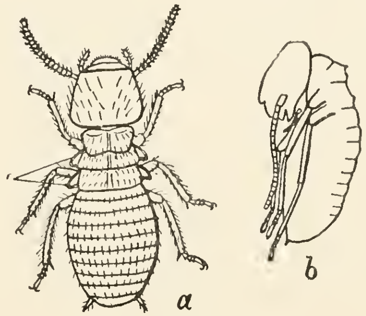



FIG. 44.

*a*, Early larva of North Indian Termite (*Archotermopsis*) with wing-rudiments (*r*). × 5. After Imms, *Phil. Trans. R.S.*, 1920; *b*, resting larva of Termite (*Rhinotermes*), lateral view. × 5. After Holmgren, *Zool. Jahrb. Syst.* XXIII.

and without feeding (Fig. 44 *b*). In some cases it lies on its side in a chamber or passage of the nest with the head bent ventralwards and the feelers directed backwards alongside the legs. This condition is noteworthy, for it suggests the pupal stage in the life-history of such insects as butterflies and beetles. And it may suitably lead on to the consideration of some insects of other groups, in which such a resting-stage forms a constant and prominent feature, although they conform to the same visible type of wing-growth.

Gardeners are familiar with small elongate insects, known commonly as Thrips, which often live in numbers on the leaves and blossoms of plants, whence they suck sap, often causing thus considerable injury. They form a special order (the Thysanoptera[1]) characterized by the curious feelers with

[1] H. Uzel: "Monographie der Ordnung Thysanoptera". Königgratz, 1895. W. E. Hinds: "Thysanoptera inhabiting North America." *Proc. U.S. Nat. Mus.* xxvi., 1902.

seven or eight bead-like segments, the sucking conical mouth with the pair of mandibles and the left maxillary blade modified as piercers, both maxillary and labial palps (absent in the Hemiptera) being present. The short feet ending in bladder-like suckers, have no claws, and the wings, usually present, are very narrow, each with only one or two nervures and fringed with exquisitely delicate and slender bristles. The abdomen, spindle-shaped or cylindrical, tapers to the tail-end (Fig. 45), and bears usually, in the female, a cutting ovipositor.

Such an insect, often with its hardened cuticle shining black, a small active creature perhaps only a millimetre in length, lays, in incisions cut in leaves, little whitish rounded eggs

FIG. 45. BEAN THRIPS (*Heliothrips fasciatus*). × 36. After Russell, *Entom. Bull.* 118, *U.S. Dept. Agric.*

(Fig. 46 *a*) whence the young thrips are in due time hatched. These attain in their first stage (Fig. 46 *b*), a length about half that of their parent, which they resemble in general body-form, but their colour is translucent white and there is no trace of wings. After the first moult, the insect becomes almost as large as the parent, yellowish white in colour, possibly with crimson spots and still entirely wingless (Fig. 46 *c*). The third stage shows the same general shape and colour, but the body is somewhat strongly bristly, and conspicuous wing-rudiments reach backwards as far as the third abdominal segment (Fig. 46 *d*). After the third moult the creature appears in its last stage but one (Fig. 46 *e*), bristly, with narrow,

elongate wing-rudiments which extend as far as the seventh segment of the hind-body. This is the characteristic resting-stage in the life-history; the feelers lie backwards resting on

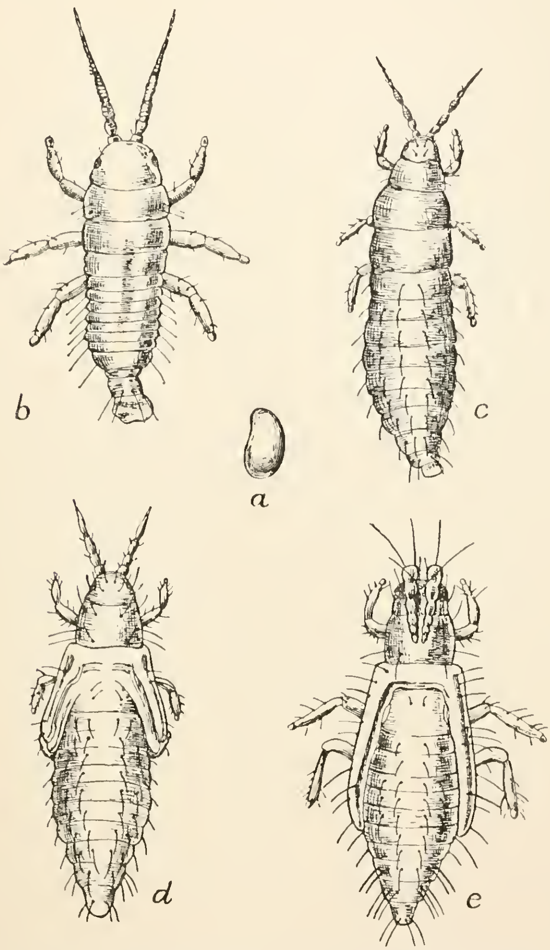


FIG. 46. DEVELOPMENT OF BEAN THRIPS (*Heliothrips fasciatus*). *a*, egg; *b*, *c*, first and second instars; *d*, nymph with wing-rudiments; *e*, resting nymph ("pupa"). × (*a*) 40, (*b*) 70, (*c*, *d*, *e*), 45. After Russell, *Ent. Bull.*, 118, *U.S. Dept. Agric.*

the dorsal aspect of the head and prothorax, and the insect remains quiet and motionless until the final moult ushers in the adult winged condition.

For further and more specialized examples of this type of life-history we may return to the order (Hemiptera) of the bugs and greenfly, and take one or two families of the same group as the latter. The Snowy-flies (*Aleyrodidae*)[1] are a

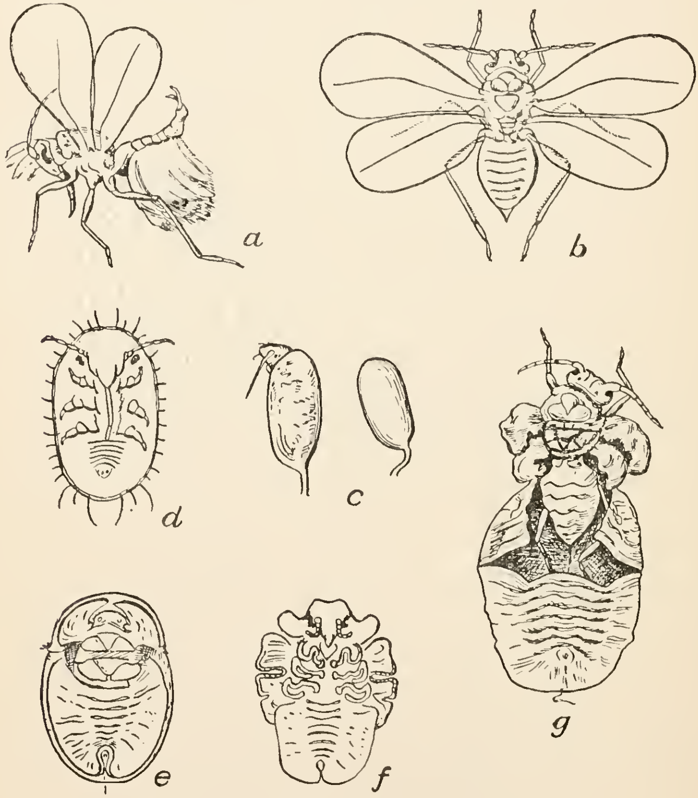


FIG. 47. SNOWY-FLY (*Aleyrodes citri.*)
*a*, male (side view); *b*, female (dorsal view); *c*, eggs (one with larva hatching); *d*, first-stage larva (ventral view); *e*, cuticle of second instar; *f*, "pupa" (rests within cuticle of third instar); *g*, adult (with crumpled wings) emerging. × (*a*, *b*, *e*, *f*, *g*) 16; (*c*, *d*) 60. After Riley and Howard, "Insect Life", V.

family of little insects with white wings, sometimes present in large numbers on plants whose sap they suck. In these countries only a few species occur commonly out of doors, but they often appear as pests in greenhouses. The head, with

[1] A. L. Quaintance and A. C. Baker: "Classification of the Aleyrodidæ". *U.S. Dept. Agri. Entom. Tech. Series* No. XXVII. 1913-14. "Contribution to our Knowledge of the White Flies". *Proc. U.S. Nat. Mus.* Vol. LI. 1917.

small but prominent compound eyes at the sides and two ocelli on the crown, bears a pair of feelers usually with seven segments and of the aphid type. The prothorax is short, the mesothorax large and convex with a pair of comparatively ample, rounded wings, with reduced nervuration and snowy-white in hue ; the hindwings, similar in appearance, are somewhat shorter and narrower than the forewings. The legs are slender with two-segmented feet, each foot carrying two claws and a bristle-like median process (*empodium*). The male's abdomen has a pair of conspicuous claspers ; that of the female tapers to the tail-end whence project the pointed process of the ovipositor. Frequently these insects are partially covered with a white, waxy secretion in the form of long threads (Fig. 47 *a*). The colour of the cuticle is commonly yellowish.

The eggs (Fig. 47 *c*) laid by the female *Aleyrodes* are remarkable for the long stalks by which they are fastened to a leaf of their food-plant. The young insect hatched from one of these eggs is a characteristic larva (Fig. 47 *d*), strikingly unlike its parent, the body flattened in form with indistinct segmentation and an oval margin fringed with bristles, the short legs, with undifferentiated shin and foot segments and no claws, not being visible from above, while the feeler has only three segments. This tiny larva—only about a quarter the length of its parent—moves actively about and feeds until the time arrives for the first moult ; this is brought about, after preliminary up-and-down movements of the abdomen, by a splitting of the cuticle at the front edge so that the insect gradually works its way out, the old cuticle slipping off backwards. The second-stage larva (Fig. 47 *e*) is of the same general form as the first, but the legs are very short and rudimentary so that the creature becomes sluggish in its behaviour —a condition which persists into the third stage, like the second but larger—the insect being now half as long as the adult. Throughout the larval stages no trace of wing-rudiments is apparent. The final larval instar (third or fourth) after a short period of feeding settles down on a leaf to which its body-margin is closely applied, and the cuticle separates from the underlying skin without being shed. Wing-rudiments then grow out from the second and third thoracic segments ;

the new cuticle grows over these, and thus is formed a quiescent nymph or " pupa " (Fig. 47 *f*), lying hidden and protected by the hardened larval-cuticle or " pupa-case ". From this in due time the imago emerges, the case opening with a dorsal T-shaped slit through which the fly comes forth having already worked off the delicate nymph-cuticle (Fig. 47 *g*). The thorax first appears, followed by the head; then are withdrawn the feelers and legs, and finally the abdomen.

From this brief account of the development of the snowy-flies, it will be seen that they pass through a marked transformation in the course of their life-history. The way in which the appearance of the wing-rudiments is postponed until the last stage but one agrees with what happens in the life-history of the butterfly; and were these wing-rudiments growing inwards during the larval stages, the snowy-flies would have to be included among those insects that practise the hidden type of wing-growth. Their structure, both larval and adult, shows that they are nearly related to families of insects—the Suckers (or *Psyllidae*) for example—in which the open type of wing-growth is evidently the rule; thus they afford an interesting and suggestive intermediate condition, the importance and significance of which will be discussed in the last chapter of this volume.

Another family of sucking insects allied to the snowy-flies afford us also examples of a type of life-history very similar, but complicated by a striking divergence between members of the two sexes when adult. These are the *Coccidae*,[1] including the Scale-insects and " Mealy-bugs ". The tiny males (Fig. 48 *a*) in this family have long, jointed feelers and comparatively ample forewings, so that they are active fliers, but the hindwings are modified into short, twisted, thread-like organs, and the beak and piercers are so much reduced that the insect takes no food after attaining the winged condition. The newly-hatched larva (Fig. 48 *c*), oval in form, resembles somewhat that of a snowy-fly, but has the segmentation of the body better marked and the feelers and legs more typically developed; the beak is short and conical; the piercers, very

[1] R. Newstead: " Monograph of the Coccidae of the British Isles ". London, 1901-3. A. D. MacGillivray: " The Coccidae ". Urbana, Illinois, 1921.

long and flexible, may be driven deeply into the plant-tissues. After a period during which it walks about with fair activity, the larva fastens itself by its piercers and remains quiescent, a protective waxy secretion forming over the body, white, diffuse and thread-like in the mealy-bugs, but reinforced with the cast cuticle and hardening into the characteristic shield-like scale in the typical scale-insects (Fig. 49). Beneath this the young male (Fig. 49 *d*) passes into a second larval form without feelers or legs,[1] but rudiments of these as well as of

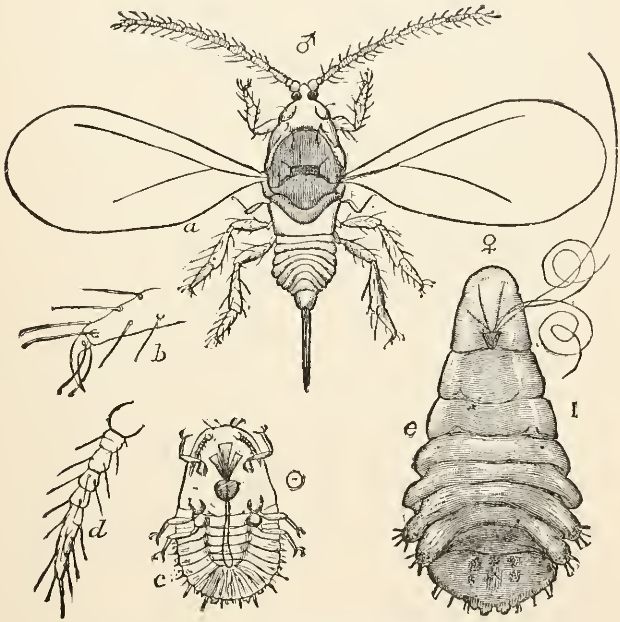



FIG. 48. MUSSEL SCALE-INSECT (*Mytilaspis pomorum*).
*a*, male (dorsal view); *c*, nymph; *e*, female (ventral view). × 40. *b*, Foot of male; *d*, feeler of larva. Highly magnified. From Howard, *Year Book, U.S.A. Dept. Agric.*, 1894.

wings are prepared in the underlying body-wall, to appear outwardly in the next stage of the life-history, the so-called "pupa" which remains still beneath the shelter of the scale until the fully developed, winged adult emerges, breaking through both pupal cuticle and scale to the enjoyment of its short existence as a flying creature of the air.

[1] E. O. Schmidt: "Metamophose und Anatomie des männlichen Aspidiotus nerii". *Arch. f. Naturgesch.*, LI. 1885.

Very different is the fate of the larva destined to develop into a female scale-insect. Resembling closely the male larva during the first stage, she passes into a similar quiescent condition beneath a protective scale of distinctive form (Fig. 49 *a c*). For the rest of her life she remains with feelers and legs vestigial or absent, her body increasing in size so that she becomes considerably larger than her mate, but with the development so arrested or degraded that when the adult state is

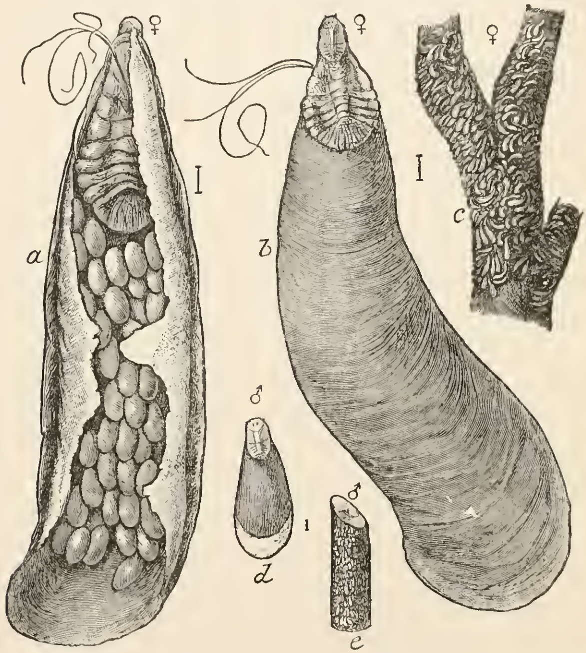



FIG. 49. MUSSEL SCALE-INSECT (*Mytilaspis pomorum*).
*a*, female (ventral view) showing eggs protected by "scale"; *b*, female (dorsal view). × 24. *d*, male "scale," × 12. *c*, female, and *e*, male "scales" on twigs, natural size. From Howard, *Yearbook, U.S. Dept. Agric.*, 1894.

attained she seems to be little more than a limbless egg-bag. Among the "mealy bugs"—members of the genera *Dactylopius* and *Pseudococcus* for example—the female (Fig. 50) does not lose her feelers and legs; she is able, therefore, to move about and, though she never acquires wings, she does not undergo the extreme degeneration noticeable among the true scale-insects. The waxy secretion forms a threadlike or felted covering for the female's body, often extending over the eggs

as a protective hood or ovisac. In rare instances the male as well as the female is wingless, and it is of great interest to find in such a case (the species *Apterococcus fraxini* for example) that the resting " pupa ", so characteristically associated with wing-growth, occurs as the penultimate stage of the life-history although wings are never developed in either sex.

There is yet another order of insects, illustrating the open type of wing-growth, to which reference may now be suitably made, as they exhibit not a few features that throw light on some of the larger problems raised by a study of insect transformations. These are the mayflies (Ephemeroptera),[1]

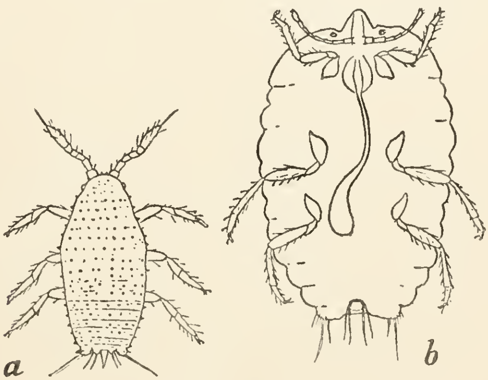



FIG. 50. MEALY-BUG (*Pseudococcus aceris*).
*a*, larva (dorsal view); *b*, female (ventral view). × *a*, 45; *b*, 20. After Carpenter, *Econ. Proc. R. Dublin Soc.* II.

creatures whose life-history involves, like that of the dragon-flies described in the preceding chapter, a transition from water to air, though they offer in many respects a striking contrast to the latter group. Mayflies (Fig. 51 *A*) are delicate, fragile insects with the jaws so excessively reduced that they are unable to feed, differing thus as widely as possible from the dragon-flies, those voracious hunters of the air. A mayfly's compound eyes are large and prominent, each eye divided, in some males, into two regions, the inner of which crowns an outstanding, pillar-like prominence of the head; there are also three simple eyes (*ocelli*). The feeler is short, consisting

[1] A. E. Eaton: " A Revisional Monograph of Existing Ephemeridæ or Mayflies ". *Trans. Linn. Soc.* (*Zool.*) (i), III. 1882-5. L. C. Miall: " The Natural History of Aquatic Insects ". London, 1895.

of two short basal segments and a third elongate and stiff, suggesting a fine bristle.

In the mayfly's thorax the first segment is small, the second segment (*mesothorax*) dominating this region of the body and bearing a pair of wings, subtriangular in shape and relatively ample in extent, with a nervuration in which all the typical longitudinal trunks are usually present, while numerous cross-nervules make a complex network. The third segment (*metathorax*) is short, the hindwings being small, with the nervuration somewhat reduced. The legs are relatively long and slender, the number of foot-segments being very variable —from one to five ; in some male mayflies the forelegs are of exceptional length.

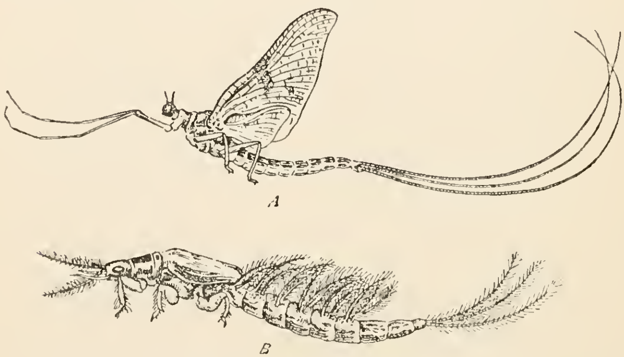



FIG. 51. MAYFLY (*Ephemera*).
*A*, male ; *B*, nymph. Side view. Somewhat enlarged. From Comstock "Introduction to Entomology", after Needham.

The abdomen is elongate and narrow with a pair of long, jointed tail-feelers (*cerci*) on its tenth segment and, in some genera, a median jointed process between these. It has been stated that a mayfly takes no food ; nevertheless its digestive tube is present with the normal regions—gullet, crop, stomach, and intestine—recognizable. The walls of this food-canal are very thin, and the stomach becomes swollen with air which, swallowed through the mouth, is confined by the action of valves at either end of the mid-gut. The reproductive organs are of a simple and primitive type, the paired oviducts of the female opening separately to the exterior behind the seventh abdominal segment, instead of passing into a median vagina,

lined with cuticle, as is usual in insects. Similarly the genital ducts (*vasa deferentia*) of the male open separately on the ninth abdominal segment.

Mayflies are to be observed in large swarms over the surface of lakes and streams. The air-filled stomach is supposed to render the insects buoyant and also to facilitate the discharge of the eggs by dilating and pressing against the ovaries. The aerial dances of the mayfly swarms, through their short lives, over the waters that serve as their breeding-places, have often been described. After pairing the female drops on the water her eggs in clusters, which subsequently break up so that the eggs are scattered about the bottom of the stream or lake; or she rests at intervals on the surface film, allowing a few eggs to fall on each occasion. From the mayfly's egg is hatched a larva (Fig. 51 *B*) which lives in the water for a period that seems excessively long when compared with the short life of the winged adult, for these insects may take a year or two for the completion of their transformations. The mayfly larva has a firmer cuticle than its parent, which it resembles in possessing a pair of tail-limbs (*cerci*) and six well-developed thoracic legs, while its feelers are relatively much longer than those of the perfect insect and often many-jointed. The relatively broad head and thorax and the tapering abdomen, give to the mayfly larva (Fig. 52 A C), in conjunction with the conspicuous appendages just mentioned, the appearance of a wingless insect belonging to the Thysanura (Figs. 96, 97) or Bristle-tails. And examination of the jaws shows that this likeness is not merely superficial, for the mayfly grub has mandibles (Fig. 53 *a*) which with their elongate basal region and median grinding area, resemble—as those of bristle-tails do—the mandibles of certain Crustacea more closely than those of typical insects, while attached to each side of the dorsal aspect of the tongue is a relatively large and prominent maxillula (Fig. 53 *b*). With such jaws the mayfly grub masticates its food which consists largely of organic fragments that may be in the mud wherein many of these larvae live, and which they swallow in considerable bulk. Others, however, crawl beneath submerged stones in swift streams and prey upon other insects.

Living, as it does, submerged in water, the mayfly larva has

like the dragon-fly grub, to depend on dissolved air for its supply of oxygen. The newly-hatched insect (Fig. 52 A) has no special breathing organs, the necessary gaseous exchange

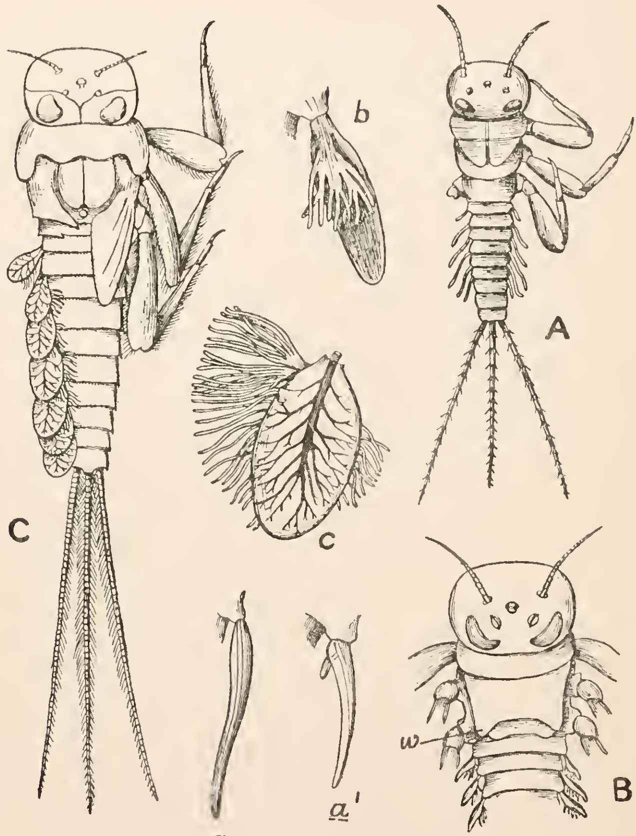



FIG. 52. MAYFLY LARVAE AND NYMPHS (*Heptagenia*).

A, Third instar. × 16. a, abdominal appendage; $a^1$, abdominal appendage of instar. × 45. B, Front region of seventh instar with small wing-rudiments (*w*). × 12. *b*, an abdominal appendage. × 45. C, Eighth instar with prominent wing-rudiments (legs are shown on right, abdominal gill-appendages on left). × 4. *c*, a gill-appendage. × 15. After Vayssière, *Ann. Sci. Nat. Zool.* XIII.

being carried on through the delicate cuticle. In the genus *Cloeon* there are over twenty moults during the life-history.[1] In the third instar seven pairs of appendages are evident

[1] J. Lubbock: " The Development of Chloeon ". *Trans. Linn. Soc., Lond.*, XXIII. 1863.

on the abdominal segments from the second to the eighth inclusive. These are at first slender and elongate (Fig. 52 *a*); after several moults they are seen to be flattened in form and traversed by a set of branching air-tubes (Fig. 52 *c*) continuous with the tracheal system of the larva. These are the characteristic leaf-like abdominal gills of the mayfly grub, each pair attached laterally to the hinder edge of the segment. In some cases projecting into the water from the margin of the abdomen, in others lying over the back, these gills are in frequent motion, and, surrounded by water, are efficient organs of gaseous exchange; delicate, elongate bristles are seen to fringe them in the typical Ephemerae.[1] As these gills are usually flattened in form, dorsal in position, and traversed by air-tubes they have been compared[2] to the wings borne on the thoracic segments. Recent investigations[3] into their structure, musculature and development[4] show, however, that their true correspondence is rather with the insect's legs, that they are indeed the limbs of the abdominal segments which bear them, specially modified for the function of breathing, and that they indicate thus a further parallel between mayfly grubs and bristle-tails, many of which carry a series of abdominal limbs. In some mayfly larvae the tail-feelers (*cerci*) also are used as breathing organs, the chamber of the heart in the hindmost segment sending into them delicate arteries through which the blood is propelled, escaping through small holes into the extension of the blood-space which forms the cavity of the appendage, which thus becomes a blood-gill, effecting gaseous exchange through its delicate cuticle with the dissolved air.[5]

The mayfly grub may show no trace of wing-rudiments till it reaches the eighth or ninth stage of its life-history; then these

[1] A. Vayssière: "Récherches sur l'Organization des Larves des Ephemerides". *Ann. Sci. Nat.* (*Zool.*), (6) XIII. 1882.

[2] C. Gegenbaur: "Grundriss der vergleichende Anatomie". Leipzig. 1878.

[3] C. Börner: "Die Tracheenkiemen der Ephemeriden". *Zoolog. Anz.* XXXIII. 1909.

[4] R. Heymons: "Grundzüge der Entwicklung und des Körperbaues von Odonaten und Ephemeriden". *Abhandl. K. preuss. Akad. d. Wissensch. Berlin.* Anhang. 1896.

[5] O. Zimmermann: "Ueber eine eigentümliche Bildung des Rückengefasses bei einigen Ephemeridenlarven". *Zeitsch. f. wissensch. Zoolog.* XXXIV. 1880.

structures appear as backwardly-directed, dorso-lateral outgrowths of the second and third thoracic segments (Fig. 52 B). They become larger after each succeeding moult, and the young insect may now be termed a nymph. The development of wings in the aquatic mayfly nymph does not differ in any important respect from the same process in dragon-flies and other insects with the typical open type of wing-growth already described. But with the passage from water to air some striking peculiarities are to be noticed. When the nymph leaves the water the moult is often exceedingly rapid,

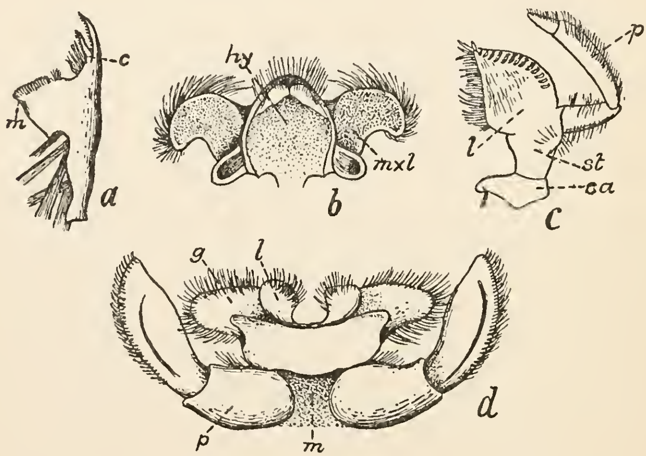



FIG. 53. JAWS OF NYMPHAL MAYFLY (*Heptagenia*).
*a*, mandible (*c* apical teeth ; *m*, molar area) ; *b*, tongue (*hy*) and maxillulae (*mxl*) ; *c*, maxilla (*ca*, cardo ; *st*, stipes ; *l*, lobe ; *p*, palp) ; *d*, labium (*m*, mentum, ; *l*, lacinia ; *g*, galea ; *p*, palp). × 10. After Vayssière, *Ann. Sci. Nat. Zool.* XIII.

so that the winged insect may fly away less than half a minute after the nymph-cuticle has begun to split ; naturally the cuticle of the newly-emerged mayfly is very thin and delicate.

But now ensues a feature which makes the life-history of mayflies different from that of all other insects. The winged creature which has left the old nymph-husk resting on the surface of the water is not the adult. It is a *sub-imago*, which after flying about for a few hours, or perhaps for a shorter period, casts off its delicate cuticle that clothes the wings as well as the body and legs, and thus becomes transformed into

the fully-developed mayfly (or *imago*) ready for its brief life of mating and egg-laying. No other insects besides mayflies undergo a moult after having attained the power of flight, and this feature, in conjunction with some of the larval peculiarities just set forth, makes the life-history of mayflies of surpassing interest to the student of insect transformations. The importance of these features and their bearing on the problems of insect life-histories will be better appreciated and discussed after some examples of the hidden type of wing-growth shall have been passed in review.

## CHAPTER IV

# THE HIDDEN TYPE OF WING-GROWTH

IN our second chapter we emphasized the distinction that may be drawn between the open and the hidden types of wing-growth in insect life-histories. We turn now to consider some details of the latter type as they are exhibited by various insects suitable for comparison with the butterfly, its pupa, and its larva the caterpillar, which served as our example of the type in that preliminary study. It will be convenient to take these details in three sections and to discuss, firstly: some typical modifications among insect larvae; secondly: differences in the form and behaviour among pupae; and thirdly: variety in the changes undergone by the internal organs, including the inwardly-growing imaginal buds of the larva.

### (*a*) SOME FORMS OF LARVAE

At the close of the second chapter it was pointed out that the contrast between butterfly and caterpillar, though superficially striking, should not be exaggerated and that among other insects which practise what we define as the hidden type of wing-growth, a graded series illustrating various degrees of divergence between imago and larva can be readily demonstrated. In many insects the larva differs less from the imago than the caterpillar from the butterfly; in many again it differs much more.

The beetles afford an excellent introduction to the study of this subject because among them great differences in the modification of larval form may be observed.[1] They are to be regarded as a well-marked order of insects whose name

[1] J. C. Schiodte: "De Metamorphosi Eleutheratorum". *Naturhist. Tiddskrift*, I-XIII. 1861-1883.

(Coleoptera) indicates the transformation of the forewings into firm, hard sheaths (*elytra*, Fig. 56 *g*) beneath which the delicate, membranous hindwings can be folded and protected when not in use for flight ; in many beetles indeed the hindwings are so poorly developed as to be useless ; such never fly at all and their strong, horny forewings (elytra) have become a kind of armoured deck, roofing over the hind-body. Beetles have jaws adapted for biting ; the mandibles and maxillae are essentially like those of a grasshopper, but the appendages which form the labium (Fig. 54) are much more intimately joined together than in the latter, so that the two inner lobes (*laciniae*) form a median process (*ligula*) while the outer lobes (*galeae*) are small and inconspicuous. Beetles are remarkable for the elaboration of their exoskeleton, the various

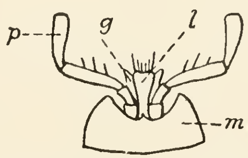



FIG. 54. LABIUM OF A GROUND BEETLE (*Carabus*).
*m*, mentum ; *l*, ligula (united laciniae) ; *g*, galea ; *p*, palp. × 8.

sclerites of which, generally firm and rigid, are precisely fitted together, so that the whole insect may be described as particularly well-armoured.

When describing in the preceding chapter (pp. 91–7) the life-history of mayflies, the likeness of the mayfly larva to a thysanuran or bristle-tail was pointed out. From the name (*Campodea*) of a common bristle-tail has been derived the term *campodeiform*[1] often applied to such elongate, well-armoured larvae, with comparatively long feelers and legs, often provided with a pair of tail-feelers (*cerci*) at the hinder end of the body. Examples of campodeiform larvae are afforded by several families of beetles. We may take in the first place the grub of a ground-beetle (*Carabid*). This larva (Fig. 55) which, like its parent-beetle, usually feeds on small

[1] F. Brauer : " Betrachtung über die Verwandlung der Insekten ". *Verhandl. K. K. Zool-bot. Gesellsch. Wien.*, XIX. 1869. J. Lubbock : " The Origin and Metamorphosis of Insects ". London, 1874.

insects, has a broad, powerful head which bears on either side six simple eyes (*ocelli*) and a feeler of four segments, the third carrying at its tip conical, sensory tubercles. The

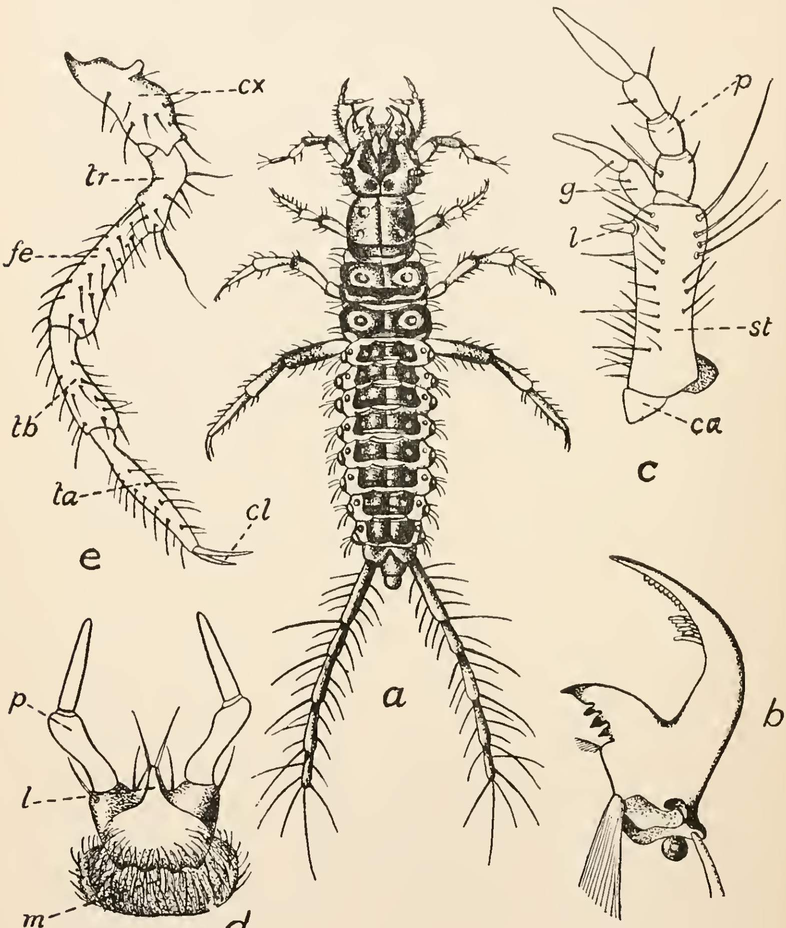



FIG. 55.
*a*, Larva of ground beetle (*Loricera*). × 8. *b*, mandible. × 60. *c*, maxilla of *Nebria* larva; *d*, labium. × 32. *e*, Leg of *Nebria* larva (*cx*, haunch; *tr*, trochanter; *fe*, thigh; *tb*, shin; *ta*, foot; *cl*, claws). × 24. After Schiodte, *Naturhist. Tidsskr.* IV.

mandible (Fig. 55 *b*) is powerful with sharply dentate apex adapted for seizing prey. Each maxilla (*c*) shows the characteristic elements, but the lacinia is reduced to a small bristle-

bearing tubercle and the galea is represented by two short cylindrical segments ; the base (*stipes*) and the palp are prominent. In the labium (Fig. 55 *d*) can be distinguished the base (*mentum*), the median ligula and the pair of short, two-segmented palps. In some ground-beetle larvae a pair of lobes representing the maxillulae can be detected. The thorax has its three segments with cuticle thick and firm ; the three pairs of legs (Fig. 55 *e*) are closely alike in structure, each being composed of haunch, trochanter, thigh, shin and foot, the last-named consisting of a single piece only, bearing two claws at its tip. Each of the nine evident abdominal segments has a strongly chitinized dorsal plate (*tergum*), a lateral sclerite on either side, and several ventral sclerites with intervening tracts of comparatively thin and flexible cuticle. The ninth segment bears a pair of stiff, bristly cerci, and between these the tubular tail-segment with the intestinal opening (*anus*) at its tip, projects backwards and downwards. As this tail-segment is used by the larva in locomotion to support the hinder region of the body it is often spoken of as an " anal proleg ". Spiracles—paired openings leading to the air-tube system—are present on the prothorax and on the abdominal segments from the first to the eighth inclusive. They are absent—as in the caterpillar (see p. 58) from the second and third thoracic segments to which the wings belong.

Such a ground-beetle larva lives lurking under stones or just beneath the surface of the soil, sallying forth, usually in the dark, to hunt for the smaller or weaker insects that serve as its prey. Among beetles of other families modifications of this campodeiform type of larva may be found. The aquatic larva of the large carnivorous water-beetle (*Dyticus*) shows this type adapted for life under water and for feeding by suction. It has a large head with long feelers and maxillary palps ; the mandibles are slender, sharply pointed and strongly curved, each with a narrow tubular channel running from tip to base where it opens at the corner of the mouth. The Dyticus grub digs these formidable weapons into the body of its victim—a small fish, a tadpole, or a weak insect—and is thus able to suck blood or other juices of its prey as food. The body is very well armoured, the sternal plates, as well as the tergal, being extensive ; the legs are long, and each foot, as in the ground-

beetle larva, carries two claws. The abdomen tapers towards the hinder end, its ninth segment being long and narrow; the cerci are stiff and fringed with hairs, their function being to pierce the surface-film of the water in which the larva lives, and thus to put a pair of tail-spiracles in touch with the upper air. The lateral spiracles along the series of body-segments are closed throughout larval life; thus the Dyticus grub affords an excellent example of the problem of an aquatic insect's breathing being solved, not—as in the case of the mayfly larva and nymph—by the development of special gill-structures, but by provision for periodical continuity between the creature's air-tube system and the atmosphere.

The larva of a rove-beetle (the adult recognized by the marked abbreviation of the elytra so that most of the abdomen is uncovered) is like that of a ground-beetle in general aspect and lives in very much the same way; but it differs in having only one claw on each foot. Such a one-clawed foot characterizes the great majority of insect larvae, whereas in the great majority of adult insects each foot has two claws. In this feature, therefore, the larvae of the ground-beetle and the great water-beetle show an unusual agreement with their adults, and this agreement is one of the characters by which a special section of the beetles (known as the *Adephaga*) is distinguished. There are, however, other families of beetles whose larvae, though they have only one claw on the foot, agree with the adult insects in some other respects.

For example, the elongate leaf-eating Silky Beetle (*Dascillus cervinus*) has a root-feeding larva (Fig. 56, *a*) which may be regarded as belonging to the campodeiform type though short and stout in build compared with the beetle grubs already described. The Dascillus larva has a very broad, prominent head, and a body which tapers but slightly to the tail-end, the terminal segment truncated and bearing a pair of very short, stiff processes. The cuticle on all the segments is strongly chitinized so that the larva has a firm, hard exoskeleton which, in conjunction with its stout, spiny legs, adapts it well for working its way through the soil. These legs have, as already implied, only one claw on the foot; it is in certain features of the jaws[1] that the larva displays its striking correspondence

[1] G. H. Carpenter and M. C. MacDowell: "The Mouth-parts of some Beetle Larvæ". *Quart. Journ. Microsc. Sci.*, LVII. 1912.

with an adult beetle—a correspondence accompanied by some remarkable primitive characters. The mandible (Fig. 56, *c*) is strong and formidable, pointed at the tip, with cutting teeth

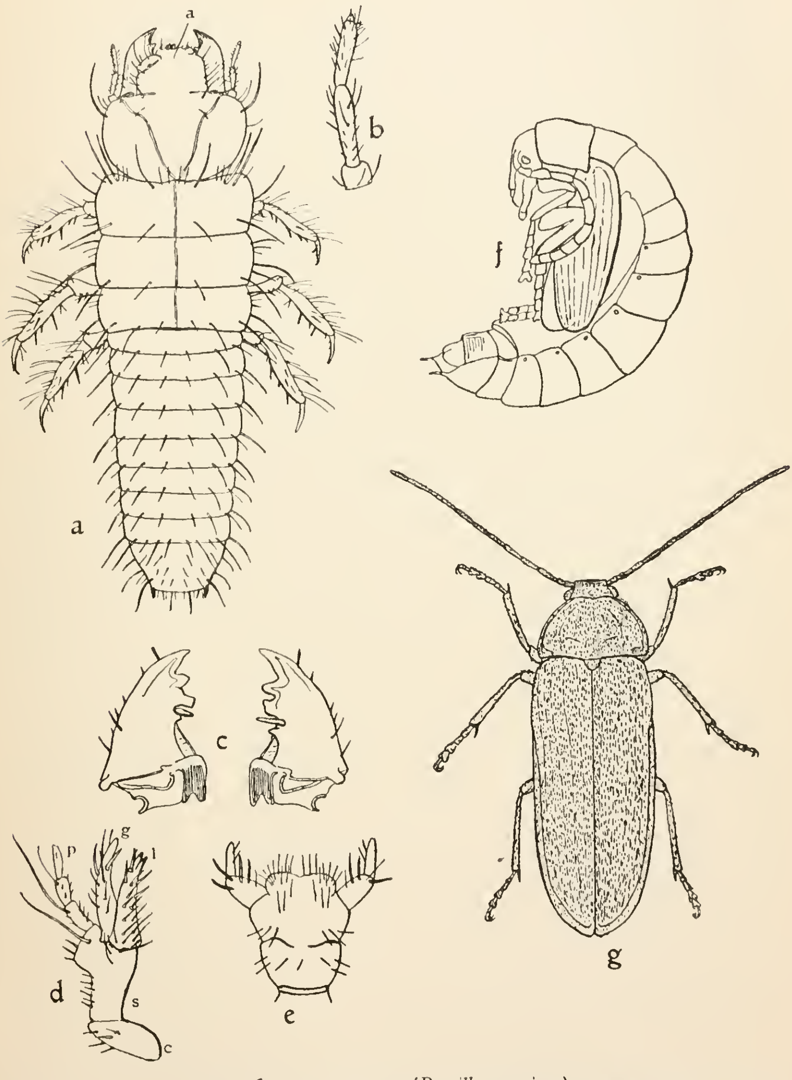



FIG. 56. SILKY BEETLE (*Dascillus cervinus*).

*a*, larva. × 5. *b*, feeler of larva; *c*, mandibles; *d*, maxilla (*c*, cardo; *s*, stipes; *l*, lacinia; *g*, galea; *p*, palp); *e*, labium. × (*b*, *d*, *e*) 15; (*c*), 10. *f*, pupa (side view); *g*, adult beetle. × 5. From Carpenter, *Econ. Proc. R. Dublin Soc.* I.

on the inner surface as well as a slender movably articulated tooth or spine (*prostheca*); at the base of the inner aspect is an extensive molar or grinding area. The maxilla (Fig. 56, *d*) conforms with remarkable closeness to the type found in adult biting insects; there is a stout, horizontal cardo (*c*) to which is jointed the broad, spiny stipes (*s*) bearing a narrow bifid lacinia (*l*), a sharply pointed galea (*g*), and a three-segmented palp (*p*). In the ground-beetle larva it will be remembered that the maxilla is much simplified as compared with that of the adult; this condition is found among beetle larvae generally, so that the very slight divergence of the dascillid larva from the imago in this respect is especially noteworthy. The labium (Fig. 56, *e*) of this larva with its two-segmented palps does not differ markedly from that of the ground-beetle grub, except that the ligula is broadly lobate instead of narrow; the interest of the labium in the Dascillus larva is that its basal regions (mentum and sub-mentum) are clearly continuous with the cuticle of the neck-region, as they are in a grasshopper or a cockroach (see p. 11 above). The ventral sclerite of the true head-capsule lies distinctly in front of the labium, so that the latter appears to belong, without doubt, to a segment situated behind the original head; reasons have already been given (p. 12) for regarding this character as primitive. And a further primitive feature is shown by the Dascillus larva, for when the tongue (Fig. 57), a flexible chitinous plate supported by strong ridges produced backwards into "feet", is examined, a pair of prominent, rounded, toothed lobes (Fig. 57 A) are seen on its front surface; these are maxillulae—the pair of small appendages, behind the mandibles, whose presence as already explained (pp. 11–12) indicates the primitive standing of those insects in which they are found. In the Dascillus larva the maxillular teeth appear to be of service in mastication, as they lie immediately below rows of denticles within the labrum or upper lip.

To the same family as Dascillus belong a number of small beetles which live for the most part, submerged in the water of streams and ponds. These (*Helodes* and *Hydrocyphon* for example) have larvae of a curiously flattened form adapted for crawling on the under surface of stones or between the broad leaves of aquatic plants, the flattening being due to a strong development of the lateral regions (*pleura*) of the cuticle of

the body-segments which extend outwards so that the legs, though well developed, are hardly visible from above. Such a larva shows a striking likeness to a wood-louse (*Oniscid*) and is therefore known as an *onisciform* larva ; like those already described it has a firm, hard cuticle. A character in which it resembles an adult beetle more closely than any of those larvae is found in its long, many-jointed feelers. The jaws of the Helodes larva are on the whole like those of the Dascillus grub

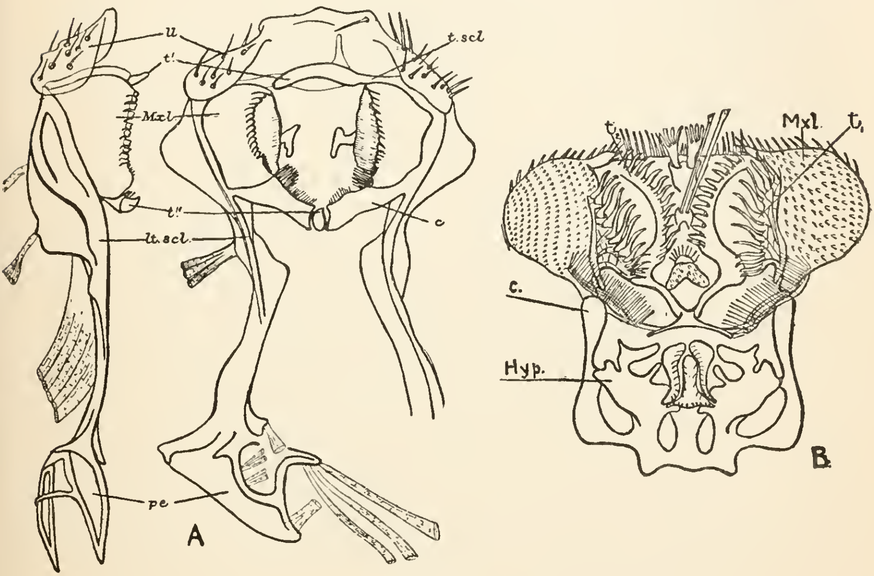



FIG. 57.

Hypopharynx and Maxillulae (*Mxl*) of (A) *Dascillus* ($\times$ 45), and (B) *Helodes* ($\times$ 90). A. *ll*, lateral lobes, and *lt*, lateral sclerites of hypopharynx ; $tt_1$, its median teeth ; *pe*, foot of hypopharynx. B, $t_1$, $t_2$, rows of maxillular teeth ; *c*, condyle. After Carpenter and MacDowell, *Quart. Journ. Micr. Sci.* LVII.

only much more delicate, and sharing in the general flattening of the body. The maxilla has cardo, stipes, lacinia, galea and three-segmented palp ; there is here some tendency to fusion between these parts, the lacinia and galea being partly enveloped in a common cuticle. The maxillulae of the Helodes larva are very perfectly developed. Each maxillula (Fig. 57 B) consists of a rounded lobe whose outer basal region articulates with a boss on the upper aspect of the broad tongue. Its surface is covered with numerous parallel rows of minute teeth

and a series of elongate, flexible teeth adorns its inner border ; its sharply pointed apex, covered with sensory hairs, projects beyond the front edges of the tongue and labium. Maxillulae have now been recognized[1] in larvae of beetles of several families.

Larvae of the general aspect just described are seen also among other families of beetles. The rotund, somewhat flattened carrion-beetles—species of *Silpha* (Fig. 58 *a*) for example—have larvae that are typically onisciform, not only resembling wood-lice in appearance but being as large as some of those interesting if familiar Crustacea. The Silpha grub (Fig. 58 *b*) has fairly long and prominent feelers, but these

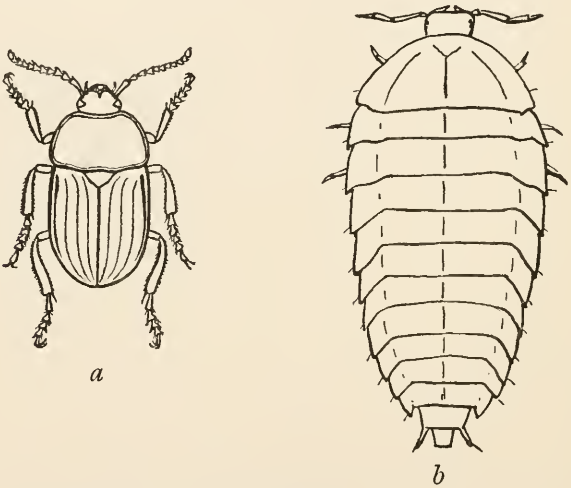


FIG. 58.
*a*, CARRION BEETLE (*Silpha opaca*). × 3. *b*, larva of *Silpha*, × 4. From Carpenter, " Life Story of Insects ".

consist of four segments only ; the maxilla (Fig. 59 *b*) has a three-segmented palp, a small but distinct hairy galea, and a spinose lacinia. Though also onisciform, these Silpha larvae do not approach the adult in their minute structure so closely as do the little helodine larvae. But on the whole all these beetle grubs that we have so far considered—with their well-developed exoskeleton and relatively long legs—may be regarded as differing less than most insect larvae from their

[1] A. M. Evans : " On the Structure and Occurrence of Maxillulae in the Orders of Insects ". *Journ. Linn. Soc.* (*Zool.*), XXXIV. 1921.

parents. Another group of beetles among which the onisciform larva is found is that of the glow-worms (*Lampyris*). And here we find between larva and parent a likeness most striking and yet abnormal, for the female beetle (the true "glow-worm" of the British countryside) never acquires wings, but becomes mature in a form closely resembling the larva.

From this we may pass on to describe beetle-larvae which illustrate an increasing degree of divergence from the parent-form. Grubs of certain click-beetles (*Elateridae*) are on account of their root-feeding habits well-known to all farmers

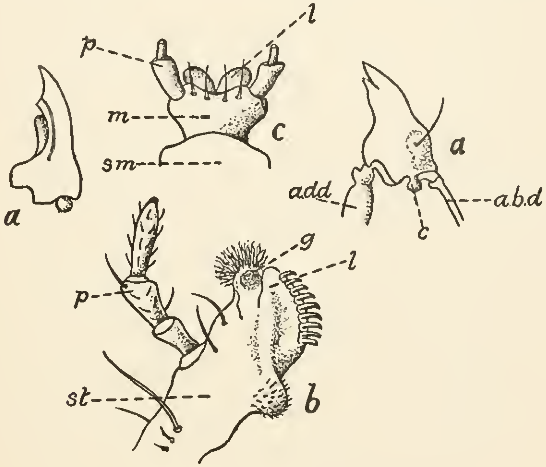



FIG. 59. JAWS OF SILPHA LARVA

*a, a,* left and right mandibles (*c,* condyle; *add, abd,* adductor and abductor tendons). × 25. *b,* maxilla (*st,* stipes; *l,* lacinia; *g,* galea; *p,* palp); *c,* labium (*sm,* sub-mentum; *m,* mentum; *l,* lobe; *p,* palp). × 32. After Schiodte, *Naturhist. Tiddskr.* I.

as "wireworms". A wireworm[1] (Fig. 60) has a narrow, elongate body with very firm hard cuticle, the dorsal aspect convex and the ventral somewhat flattened; each segment presents a longitudinal ridge and furrow on either side where the tergal and sternal regions join. The head is broad and flattened with very short stumpy feelers, but the mandibles (Fig. 6 *d*) are strong and well formed, each with apical and internal teeth and a delicate lacinia, while the maxilla (*e*) has, in addition to cardo, stipes, three-segmented palp, and two-segmented galea like those

[1] K. L. Henriksen: "Oversight over de danske Elateride Larver". *Entom. Medd.,* IV. 1911. G. H. Ford: "The Larval and Pupal stages of Agriotes obscurus". *Ann. Appl. Biol.,* III. 1917.

of the ground-beetle larva, a distinct lobate lacinia (*la*). The prothorax is distinctly the longest of the body segments, while either mesothorax or metathorax is shorter than a segment of the abdomen. The very short legs (Fig. 60 *g*) are inserted ventrally, the two of a pair rather close together towards the hinder edge of the segment to which they belong ; each leg has stout

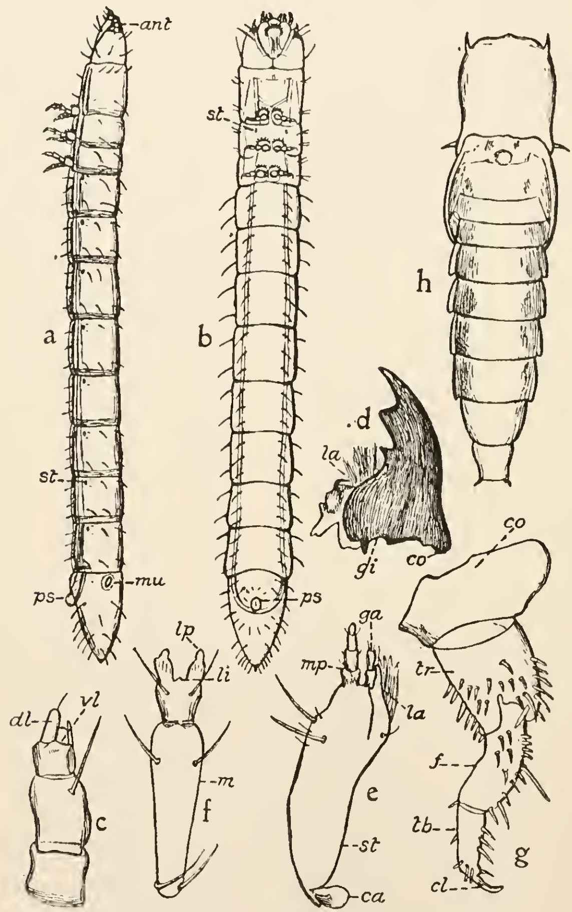



FIG. 60. "WIREWORM": LARVA OF CLICK-BEETLE (*Agriotes*).
*a*, side view ; *b*, ventral view (*ant*, feeler ; *st*, spiracles ; *mu*, muscle attachment ; *ps*, anal proleg). × 5. *c*, feeler (*dl*, dorsal ; *vl*, ventral lobe). × 65. *d*, mandible (*co*, condyle ; *gi*, ginglymus ; *la*, lacinia) ; *e*, maxilla (*ca*, cardo ; *st*, stipes ; *la*, lacinia ; *ga*, galea ; *mp*, palp) ; *f*, labium (*m*, mentum ; *li*, ligula ; *lp*, palp) ; *g*, leg (*co*, haunch ; *tr*, trochanter ; *f*, thigh ; *tb*, shin and foot ; *cl*, claw). × 32. *h*, pupa of *Agriotes* (dorsal view). × 5. After Ford, *Ann. Appl. Biol.* III.

segments, the foot, not distinct from the shin, carrying a strong claw. The prothorax and the first eight abdominal segments have each a pair of laterally-placed spiracles; on each side of the ninth abdominal segment is a large dark oval depression which looks like a spiracle but is really an ingrowth of the cuticle for the attachment of muscles. This ninth segment among the commonest wireworms (larvae of *Agriotes*) ends in a sharp conical point, but in some members of the family (*Athous* for example) its extremity is broad and bifid. Below it the tail-segment ("anal proleg", see p. 101) projects downwards. The wireworm is admirably adapted for working its way through the soil; with its wormlike shape and the marked shortening of its legs and feelers, it presents a striking contrast in form to its parent-beetle.

Another well-known beetle-grub of somewhat the same general aspect as a wireworm is a "mealworm" such as the larva of *Tenebrio,* not infrequently found living and feeding in flour and other food-stuffs. This has an elongate sub-cylindrical body similar to that of the wireworm, the head being more rounded, the feelers a little longer, and the legs more conspicuous. The cuticle, though firm, is thinner than that of the wireworm, and the ninth abdominal segment ends in two prominent, upturned, dark points. Both mealworm and wireworm display after each moult a new cuticle, pale and whitish in aspect; this becomes darker in colour as it hardens and increases in thickness.

The wireworm and the mealworm retain the hard exoskeleton of the campodeiform type of larva but differ in their wormlike aspect and their short limbs. In many other beetle grubs we find modifications in other directions: the general shape of the campodeiform larva is preserved and the legs remain relatively long, but a large part of the cuticular area is comparatively thin and flexible, a number of hard, thickened plates or tubercles on which stiff bristles or spines are arranged, forming an incomplete, but probably efficient protective armour. Thus in such a larva as that of one of our common "ladybirds" (*Coccinella*)—beetles easily recognized by their rotund form, apparently three-segmented feet, and conspicuously spotted colour-pattern—the small head-capsule is firmly chitinized, while the cuticle over most

of the body is tough and flexible, a series of firm, spine-bearing tubercles, dorsal and lateral in position, being present on each segment. The relatively long, well-formed legs enable this grub to move actively about on the leaves of plants where it hunts for the aphids and other small sucking-insects which furnish its food. Certain leaf-beetles—the little osier-eating *Phyllodectae* for example—have larvae (Fig. 61 *b*) of somewhat similar build. Here, however, the head is relatively broad, and the prothorax is completely covered by a strong tergal shield, while the other segments of the body have transversely arranged plates on the back, and groups of tubercles at the sides, all bearing stiff bristles. The Phyllodecta larva is thus well-protected and adapted for living exposed on the surface

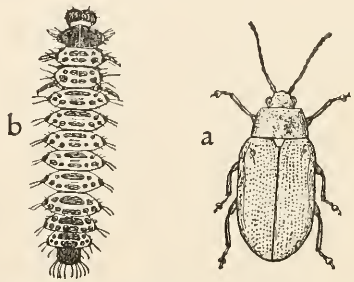



FIG. 61.
*a*, Willow Leaf Beetle (*Phyllodecta*); *b*, its larva. × 4. After Carpenter, *Econ. Proc. R. Dublin Soc.* I.

of the leaves which it devours greedily through the summer months.

From such transitional larval types we may now pass to those beetle grubs whose general aspect recalls that of the caterpillar—the *eruciform* type of insect larva as it has been termed [1] Such a grub is that of one of our common chafers: the cockchafer (*Melolontha*) or the garden chafer (*Phyllopertha*) for example (Fig 62). Here we see a stout, cylindrical grub with whitish, flexible cuticle, so strongly wrinkled that the segmentation would not be easy to make out, were not the segmentally-arranged lateral spiracles, situated as usual on the prothorax and on the first eight abdominal segments, exceptionally large and conspicuous (Fig 62 *b*). The body

[1] A. S. Packard: " A Text-book of Entomology ". New York, 1898.

of the chafer grub is usually bent like a bow, the dorsal aspect convex; this attitude is appropriate to the creature's habit of lying in an underground chamber feeding on roots. The head is large and prominent with a hard, firm, rounded capsule, bearing fairly elongate, four-segmented feelers and strong mandibles which possess not only well-developed apical biting teeth and basal grinding areas, but also, on their hinder aspect, ridged or tuberculate patches—known as "stridulating organs"—which produce a shrill sound when rubbed across by the strong teeth on the maxillary stipes. The maxilla of a chafer-grub has the typical parts well defined, though there may be partial union of the lacinia with the galea. Vestiges of maxillulae have been detected on the front aspect of the

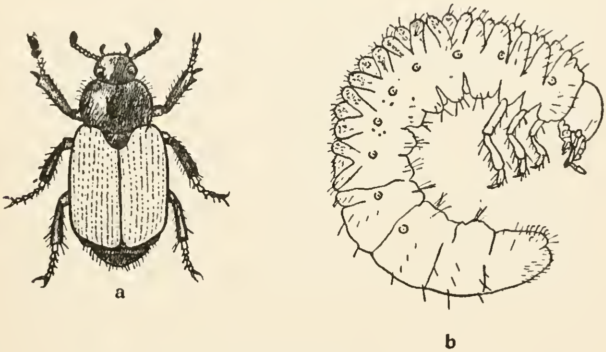



FIG. 62.
*a*, Garden Chafer (*Phyllopertha horticola*), dorsal view; *b*, larva, side view. × 3. From Carpenter, *Econ. Proc. R. Dublin Soc.* II.

tongue. The legs are prominent and hairy, remarkable for the excessive proportional length of the haunch, the thigh and shin being much abbreviated, while the foot-claw is extremely reduced in length on the third leg of the cockchafer grub and on the second leg of the larva of the garden chafer. In the larva of one of the dor-beetles (*Geotrupes*) which belong to the same family (*Scarabaeidae*) as the chafers, the legs are clawless and those of the third pair are very short and feeble in comparison with the others. In larvae of the allied tropical *Passalidae*, which live and feed in timber, the first and second pairs of legs are typical in structure while those of the third pair are exceedingly short, thickened and armed with rows

of stout teeth which scrape across a stridulating organ on the haunch of the leg next in front.[1]

The chafer grubs just described represent an eruciform type of larva in which the legs are fairly long and prominent, while in the grub of the dor-beetle a tendency to a reduction in the length of the hindmost legs is a marked feature. We may now pass to an example of the same general type in which all the

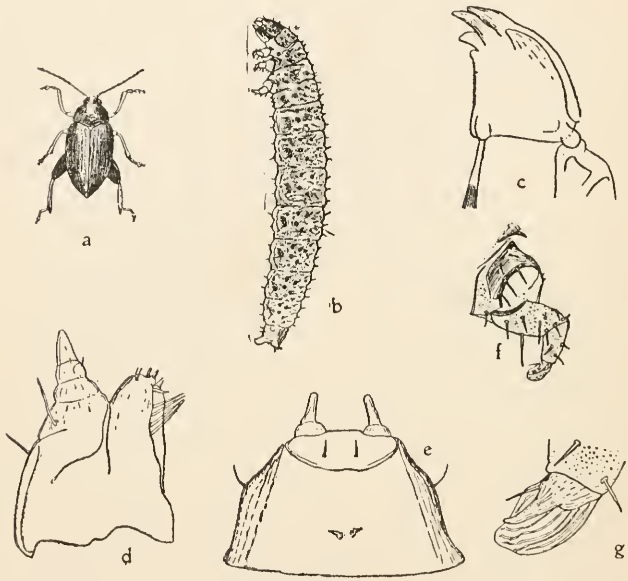


FIG. 63.
*a*, Flea Leaf-beetle (*Psylliodes chrysocephala*). × 3. *b*, larva (side view). × 5. *c*, larval mandible; *d*, maxilla; *e*, labium. × 100. *f*, leg. × 32. *g*, foot with claw and empodial appendage. × 160. After Carpenter, *Journ. Econ. Biol.* I.

legs are very short relatively to the size of the body, so that the larva's likeness to a caterpillar becomes emphasized. Such an example is afforded by a grub of a leaf-beetle of the jumping group (*Halticinae*). Of these the "turnip-flies" (*Phyllotreta*) whose larvae burrow in the green tissues of leaves are perhaps the best known; we will take the stem-boring larva of *Psylliodes chrysocephala* (Fig. 63). This has a hard and firm head-capsule like all beetle grubs, and there are

[1] D. Sharp: "Insects" in the *Cambridge Natural History*, Vols. V, VI. 1895-9 (*See* Vol. VI, pp. 192-3).

strong dorsal plates on the first thoracic and ninth abdominal segments; otherwise the entire cuticle is pale and flexible with no protective structures beyond minute tubercles bearing feeble bristles arranged in rows across the segments. The mandible (Fig. 63 *c*) is strong and toothed, while the maxilla (*d*) has fused lacinia and galea, and bears a stumpy, imperfectly jointed palp; the labium (Fig. 63 *e*) has a pair of short two-segmented palps, but its typical lobes are unrepresented. The legs (*f*) are remarkably short and stout, each consisting only of haunch, thigh and shin, the last-named segment bearing internally to the claw a delicate ridged membranous tunica (Fig. 63 *g*). As already mentioned, the ninth segment of the abdomen has a firm dorsal shield, and this is armed with two prominent hooked spines which point inwards and upwards.

A still further reduction in the relative size of the legs is seen in the stout, soft grubs of the longhorn beetles (*Cerambycidae*) which burrow in the wood of trees and feed on the timber. These larvae are broader than deep, so that a cross-section of the body is elliptical in outline. The head is very broad and strong, the cuticle hard and firm, usually of a rich brown colour. The very short feeler consists of four tiny segments. The mandible is stout and powerful, armed with robust teeth and a strong grinding area, well adapted for biting hard wood, while the maxilla has a short, three-jointed palp, and the galea and lacinia united into a convex, bristly lobe. The labium is often better developed than in the Psylliodes larva just described, as there is a ligula as well as a pair of three-segmented palps. But the legs are exceedingly small, situated on the ventral aspect of each thoracic segment, and quite invisible from above. Nevertheless, each leg often has the haunch, trochanter, thigh and shin fully recognizable and may bear a slender, pointed claw. The cuticle of the whole body is whitish and flexible, but the ninth abdominal segment may terminate in a sharp, median, backwardly-directed point (Fig. 64). In some genera of this family the legs are still further reduced so as to be mere vestiges, and in others they are completely wanting.

This condition of complete leglessness in the larva is characteristic of all the members of some large and important families

of beetles, such as the weevils (*Curculionidae*) and the bark-beetles (*Scolytidae*). The grub of a typical weevil (Fig. 65), for example, has, like the " longhorn " grub, a well-developed, hard, rotund head-capsule, while the body is covered with an uniformly flexible white cuticle, which bears a scanty clothing of feeble bristles. The feeler is short with its individual seg-

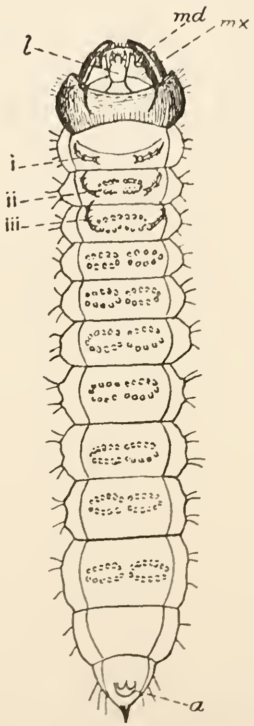



FIG. 64. LARVA OF LONGHORN BEETLE (*Rhagium*), VENTRAL VIEW. *md*, mandible; *mx*, maxilla; *l*, labium; *i, ii, iii*, thoracic legs; *a*, anal segment. × 3½.

ments (two only in number) much abbreviated. The mandible (Fig. 65 *b*) is stout and strong with robust teeth. The maxilla (*c*) has a short two-segmented palp, its galea and lacinia being merged into a single rounded lobe. The labium (Fig. 65 *d*) is compact, its palps short and thickened each with only two segments, and its ligula roundly truncated. On the ventral aspect of each thoracic segment a pair of bristle-bearing

tubercles may indicate the position of the vanished legs. The weevil grub is usually found with its soft body bent like a bow —the same attitude as that assumed by the chafer grub (see p. 111)—as these larvae live and feed within plant-tissues, whether root, stem, or leaf, or lie in earthen chambers devouring the root-fibres of plants. The white flexible cuticle is intricately wrinkled, so that the segmentation of the body cannot be traced without careful examination.

From the series of beetle larvae thus passed in review, the

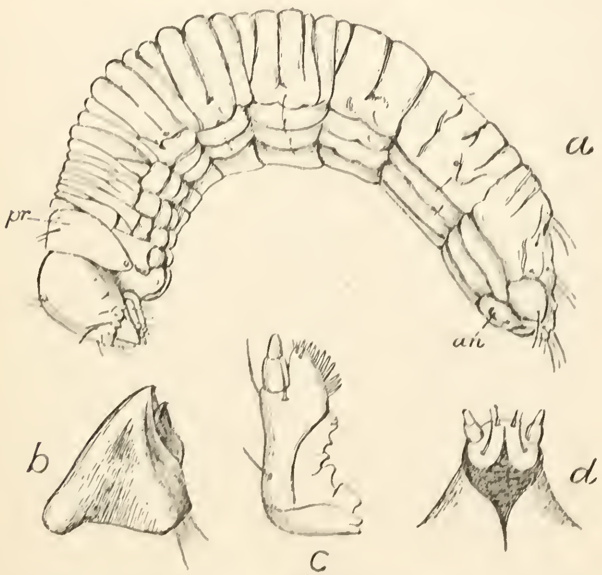



FIG. 65.

*a*, Larva of Australian Weevil (*Syagrius intrudens*), side view (*pr*, prothorax; *an*, anus). × 12. *b*, mandible; *c*, maxilla; *d*, labium. × 50. After Mangan, *Journ. Econ. Biol.* III.

student inevitably gains the conception of an increasing degree of divergence between the mature and the young insect, and realizes also how each larva has a form of body fitted to its particular manner of life. The importance of these considerations will be discussed later, but before passing from the Coleoptera to other orders of insects we must pause to call attention to the most interesting and suggestive fact that among certain beetles, different forms of larva are to be noticed in the life-history of the same insect. The oil or blister beetles (*Meloidae*)

afford an example of such *hypermetamorphosis* which has been often quoted.[1] The newly-hatched young (Fig. 66 *A*) of such a beetle is a minute larva of the typical campodeiform aspect, with well-armoured body, somewhat densely clothed with hairs, its relatively large head bearing long bristle-like feelers and sharp, prominent mandibles, and its ninth abdominal segment with a pair of elongate slender cerci, while the thoracic legs are remarkably well developed, each foot bearing two claw-like bristles in addition to the true claw, so that the tiny

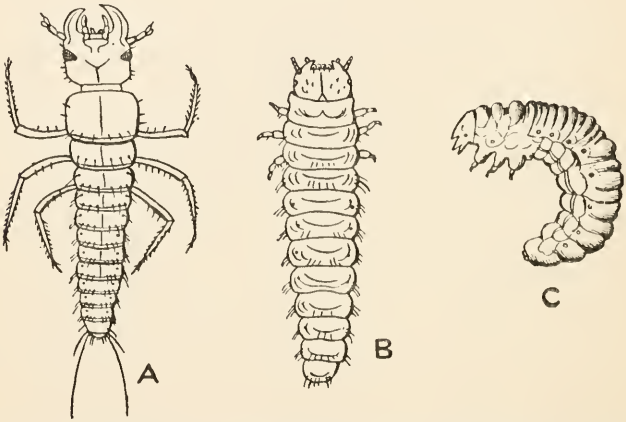



FIG. 66. LARVAL STAGES OF OIL BEETLE (*Epicauta*).
*A*, first stage (*triungulin*). ×30. *B*, second stage (*caraboid*) after moult. ×20. *C*, second stage after feeding, ready for next moult. × 10. After Riley, *Trans. St. Louis Acad.* III.

creature is known as a *triungulin*. It is well adapted for biting its way into the egg-cluster of a locust or for clinging to the body of a bee which may carry it to her nest. Arrived there the triungulin bites into a chamber containing a store of honey. On this the larva floats and feeds, having undergone a moult and assumed a form in which the body is stout with thin cuticle and the legs relatively short. This form (Fig. 66 *B*) is retained through several successive moults, until, having grown rapidly thanks to its rich food supply, the larva attains a length ten times that of the little triungulin,

[1] J. H. Fabre : " Sur l'Hypermétamorphose et les Moeurs des Meloides ". *Ann. Sci. Nat.* (4), VII, IX. 1857-8. H. Beaurégard : " Les Insectes Vesicants ". Paris, 1890.

while its comparatively tiny legs are inconspicuous. In a later stage, the larva assumes a legless condition during which it remains quiescent and does not feed; this is followed by another stage in which short legs are again evident, leading on to the pupal period and the completion of a most remarkable transformation. For the active armoured early larva,

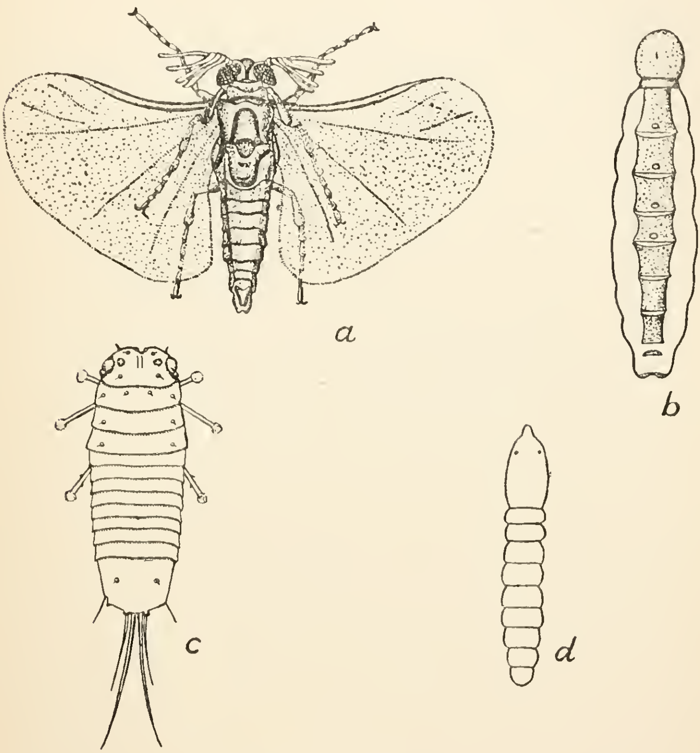



FIG. 67. STREPSIPTERA.

*a*, *Tetrozocera Santchii*, male (dorsal view). × 20. *b*, *Xenos vesparum*, female (ventral view). × 6. *c*, first-stage larva of *Stichotrema* (dorsal view). × 50. *d*, second larva of *Xenos* (dorsal view). × 6. *a* and *c*, after Pierce, *Proc. U.S. Nat. Mus.* LIV; *b*, after Berlese, *Gli Insetti*; *d*, after von Siebold, *Arch. f. Naturgesch.* IX.

like that of a ground-beetle, passes into a sluggish, soft-bodied grub like that of a longhorn or a weevil. We notice here that the campodeiform larva precedes the eruciform in the life-history, the former condition being suitable for the tiny creature's invasion of an egg-cluster or its transport through

the air to the nest of the host-bee, and the latter being assumed when it finds itself in shelter amid a rich and abundant supply of food.

A somewhat similar hypermetamorphosis is found also among the Strepsiptera[1]—very small insects whose males (Fig. 67 *a*) have the reduced forewings narrow and twisted, and the broad hindwings developed for flight, while the degraded wingless and legless females (Fig. 67 *b*) remain within the bodies of insects (mostly wasps, bees and froghoppers) in which the larvae live as parasites. The tiny first-stage larvae are active and armoured with long feelers and legs, but the feet bear suckers instead of claws (Fig. 67 *c*). Hatched within the mother's body, they emerge and crowd over the host's cuticle. Those of them which find opportunity, bore into a host-insect in the larval stage; then they moult and assume the legless, soft-cuticled form suitable to their parasitic manner of life (Fig. 67 *d*). In the subsequent life-history of the male, the most remarkable features are the development of a pre-pupal instar with wing-rudiments inside the separated larval cuticle, and the subsequent development of a pupa inside this, so that the emerging male has three cuticles to break through. The female never comes out of the hardened larval cuticle.

While the beetles exhibit great variety in the structure of their larvae, in most groups of insects we find some form that is especially characteristic of each order. If, for example, we take that assemblage of families in which the perfect insect has biting jaws much like those of beetles, but has all four wings membranous and net-veined (the order Neuroptera of most modern entomologists), we find larvae of the campodeiform type, resembling often in their general build the grubs of ground-beetles except that the characteristic cerci or tail-feelers are wanting. The larva of the alder-fly (*Sialis*), a common inhabitant of the muddy bottom of ponds and sluggish streams, has a broad head and thorax, and a long tapering abdomen, all the segments being strongly chitinized. The head carries fairly prominent, four-segmented feelers, formidable mandibles

[1] W. Kirby: "Strepsiptera, a new Order of Insects". *Trans. Linn. Soc.*, XI. 1813. W. D. Pierce: "A Monographic Revision of the Twisted-winged Insects". Bull, 66. *U.S. Nat. Mus.* 1909.

with strong, sharp teeth adapted for seizing prey, maxillae in which all the typical parts can be distinguished, and a labium with mentum, palps and ligula. The long, well-formed thoracic legs have each a definite foot-segment, marked off from the shin and carrying two claws. As this larva lives submerged, it needs special organs for breathing, and these are found in seven pairs of elongate jointed appendages attached on either side of the body at the front edge of the first seven abdominal segments; each of these slender gill-limbs is traversed by an air-tube which gives off fine branches, and two such tubes run side by side into the long, hollow tail-process, attached to the ninth abdominal segment, which also has, apparently, a similar respiratory function.

Among other families of this order, such as the "ant-lions," lacewings, and their allies, a modification of larval type is found associated with a small number of moults and a habit of feeding by suction, so that the body increases markedly in size during each prolonged stage of the life-history. As an example of this group, an Australian species of *Psychopsis*, whose transformation has recently[1] been described in detail, may be taken. The newly-hatched larva (Fig 68 *a*) has a broad, flattened, quadrate head which bears seven-segmented feelers and long, slender, acute mandibles and maxillae; the body with pale relatively feeble cuticle is no broader than the head and only about thrice as long, tapering to the tail-end. The legs are elongate, each with a single foot-segment that bears two short, pointed claws and a long sucker process. The jaws of this larva are most remarkable, the maxilla (Fig. 68 *mx*), with very small cardo and stipes and no palp, has a long, sharp, curved blade of nearly the same shape as the grooved mandible (Fig 68 *mn*) beneath which it rests so as to enclose a channel; through this juices from the insects captured and impaled are sucked into the stomach. The larvae of this group discharge no excrement, and as the first stage in Psychopsis lasts for eight months and the little creature feeds greedily except during its winter rest, its body swells to more than twice its original length and breadth, so that the head appears relatively small and the legs short as (Fig. 68 *b*) the first moult becomes due.

[1] R. J. Tillyard: "The Life-history of Psychopsis elegans". *Proc. Linn. Soc. N.S. Wales*, Vol. XLIII., pt. iv. 1918.

Through its second stage, which lasts four or five months, the larva feeds voraciously, though with long intervals for digestion between its meals, each of which may involve the absorption of an entire small caterpillar; it becomes relatively stouter

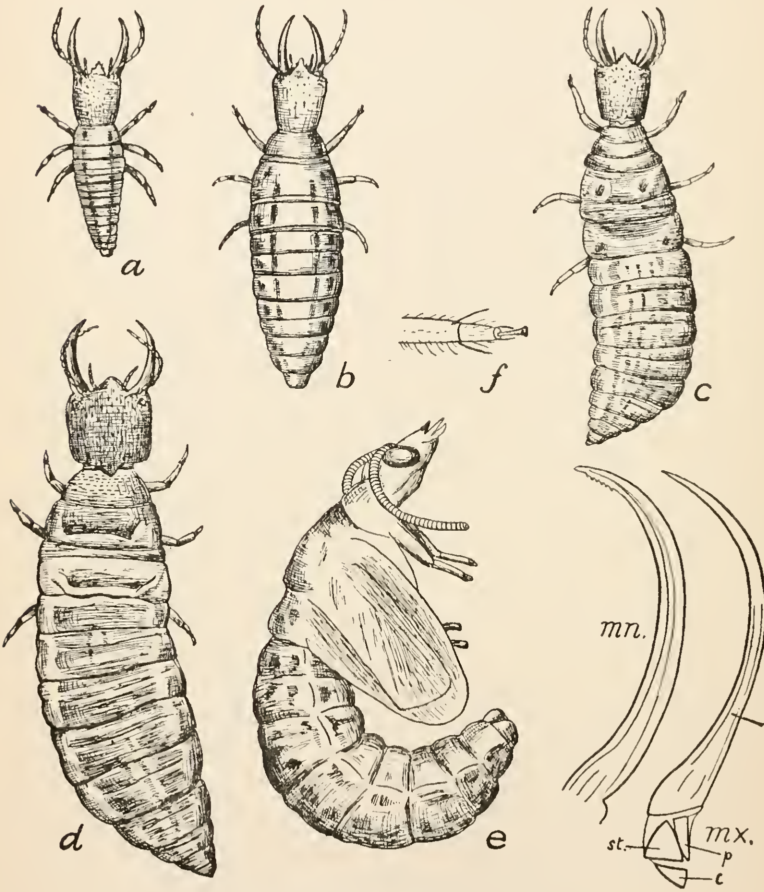



FIG. 68. STAGES OF *Psychopsis elegans*, AUSTRALIA.
*a*, young first-stage larva; *b*, the same at end of first stage. × 10. *c*, second- and *d*, third-stage larva; *e*, pupa (side view). × 6. *f*, foot of first-stage larva. × 40. *mn*, mandible; *mx*, maxilla of third-stage larva (*c*, cardo; *st*, stipes; *g*, galea; *p*, palpiger). × 18. After Tillyard, *Proc. Linn. Soc.*, *N.S. Wales*, XLIII.

as well as much longer than in the first stage, and shows a marked widening of the second and third thoracic segments as compared with the prothorax (Fig. 68 *c*). In the third stage

of larval life, the Psychopsis has a much broader head, with long feelers of nine or ten segments (Fig. 68 *d*); through all the larval stages the jaws remain of essentially the same form, the labium having a narrowly triangular base which carries long, five-segmented palps. The general form of the larval body during the third stage, which lasts nine months, is much the same as during the second. The expanse of flexible cuticle on each segment is strengthened by a pair of small, hard, brown, bristle-bearing plates. In many larvae of the group—the "ant-lions," and "aphid-lions" or grubs of the lacewing flies for example—such plates may be numerous and prominent, so that the larval body becomes quite strongly armoured.

There is a family of remarkable insects, the *Mantispidae*, allied to those just described, whose members, found in southern Europe and in the tropics, are distinguished by the possession of an elongate prothorax which carries a pair of very strong spinous front legs adapted for catching prey. From the long-stalked eggs of a Mantispa[1] are hatched typical little campodeiform larvae like the oil-beetle's triungulin (p. 116 above) these live from autumn till spring without feeding; then they penetrate into the globular egg-cocoon carried about by a female hunting spider (*Lycosa*), and attack the young spiders as they are hatched, piercing them with pointed mandibles and sucking out their juices. Such feeding leads to an expansion of the larva so that the cuticle covering its swollen body-segments becomes stretched, and it assumes the appearance of a chafer grub. Later on it undergoes a moult, and then it is transformed into a soft-bodied grub, very stout in its middle region, tapering to the tail-end, its head relatively very small, and the legs on its thoracic segments greatly reduced. In this condition it rests, amidst the dried remains of its young spider victims, until the time for its pupation shall have arrived. The life-history of Mantispa affords, therefore, like the transformation of the oil-beetles, an example of hypermetamorphosis.

Another order of insects whose larvae illustrate an interesting transitional type, are the caddis-flies (Trichoptera). These

[1] F. Brauer: "Beschreibung der Verwandlungsgeschichte der Mantispa styriaca". *Verhandl., K. K. zool. bot. Gesellsch. Wien.*, XIX. 1869.

have elongate narrow forewings and shorter hindwings, relatively broad with anal folding area, the nervuration being predominantly longitudinal ; their wings and bodies are clothed, in some cases densely, with hairs. Mandibles are wanting in the winged insects which take liquid food by means of a short, broad, sucking organ composed of the lobes of the labium ; both maxillary and labial palps are typically developed. Their larvae known as " caddis-worms " live submerged in the water of ponds and streams, breathing the dissolved air by means of delicate finger-like gills carried on certain of the abdominal segments, these gills are not, however, present on the newly-hatched larva, but appear after the first or second moult. The newly-hatched caddis grub[1] (Fig. 69 *A*) is definitely campodeiform recalling in its general aspect the larva of a rove-beetle. Its head carries short feelers, strong, toothed, biting mandibles, and maxillae and labium in which the typical parts are, as in many beetle larvæ, specialized by reduction. The cuticle of the thoracic segments forms firm dorsal plates and the legs are relatively long and well developed ; there is a foot-segment distinct from the shin, terminating in a single prominent claw. The abdominal segments have distinct dorsal plates often furnished with long, stiff bristles ; the tail-segment may carry a pair of short appendages, sometimes jointed, bearing strong hook-like claws and long flexible bristles.

At some time after hatching, varying from a few hours to several days, the young caddis begins to form a case or " house " in which it finds shelter for the rest of its larval and for most of its pupal life. Caddis-cases are composed of material varying in different families—such as plant-fragments, tiny stones, shells of water-snails—fastened together by a silk derived from glands that open, like those of moth-caterpillars, in the mouth. The important feature, in connexion with our immediate subject of modification in larval form, is that, in correlation with this sheltered mode of life, the cuticle of the abdomen becomes relatively feebler in the older than in the early caddis grub, while the thorax, thrust as a rule frequently out of the sheltering " house," retains its firm protective armour and its well-formed, jointed legs. Thus the advanced caddis

[1] A. J. Siltala : " Ueber die postembryonale Entwicklung der Trichopteren-larven ". *Zoolog. Jahrb.*, Supplement Band IX. 1907.

grub (Fig. 69 *B*) is often defined as *sub-eruciform*; it shows, like many beetle larvae a transition from the active, armoured, long-legged campodeiform larva to the caterpillar type.

The typical caterpillar, as exemplified in the larva of a moth or butterfly, has already been described with some detail in the second chapter (pp. 56–63). In such a larva the firm, thickened cuticle of the head capsule offers a strong contrast to the thin flexible cuticle that covers the rest of the usually

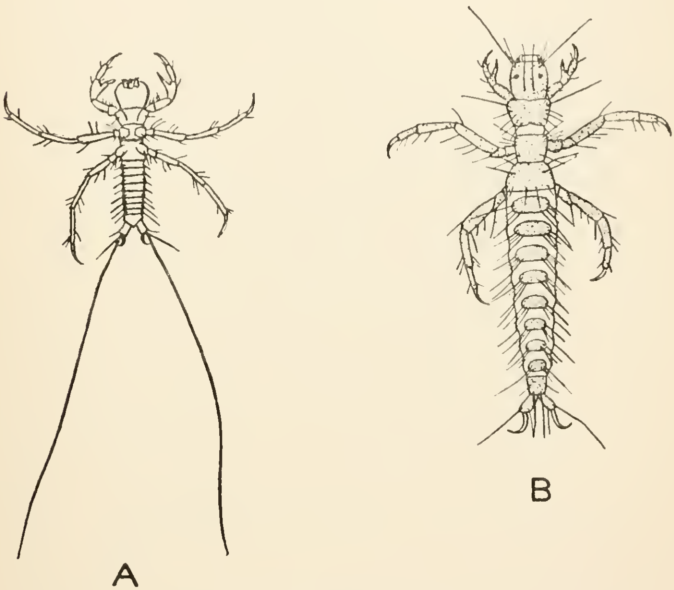




FIG. 69.
*A*, first-stage larva of Caddis-fly (*Oxyethira*), ventral view. *B*, third instar of same (dorsal view). ×20. After Siltala, *Zool. Jahrb. Suppl.* IX.

elongate, cylindrical and somewhat worm-like body. The thorax carries three pairs of short, jointed, clawed legs rather like those of the mining leaf-beetle grub already described in this chapter (p. 112). But the distinctive feature of caterpillars among other insect larvae is to be found in the presence of pairs of unjointed limbs or prolegs on certain segments of the abdomen. In the moth-caterpillar described above there are five pairs of such prolegs, the foremost on the third

abdominal segment. This is a typical arrangement among the Lepidoptera, the number of five pairs being very rarely exceeded, but in the caterpillars of some families the three front pairs of prolegs are wanting, those on the sixth and tenth abdominal segments alone being retained. Such caterpillars are frequently termed "loopers," because, the prolegs being restricted to the hinder end of the body and the jointed legs

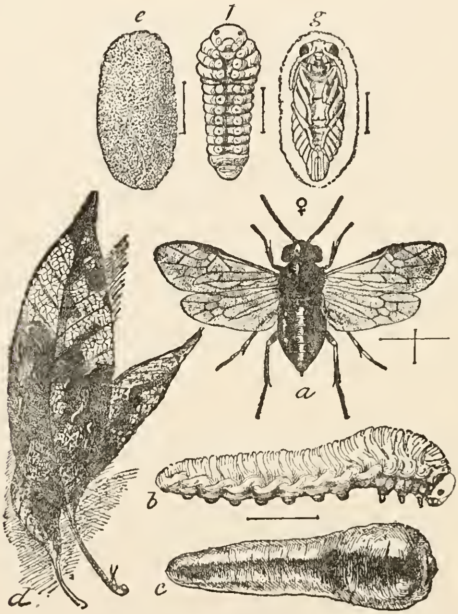



FIG. 70.
*a*, Pear Sawfly (*Eriocampa limacina*), female; *b*, larva (side view); *c*, larva with black, slimy coat (dorsal view); *e*, cocoon; *f*, resting larva (ventral view); *g*, pupa (ventral view). × 4. *d*, leaves with larvae, natural size. From Mariatt, *Ent. Circ.* 26, *U.S. Dept. Agric.*

being just behind the head, the larva alternately bends and stretches out its body as it crawls along a twig or leaf-edge.

A caterpillar is an insect larva whereof crawling may indeed be regarded as the characteristic mode of progression, and caterpillars with a greater number of pairs of prolegs than in the typical moth larva are distinctive of certain other orders of insects. For example the saw-flies—a well-marked group of the Hymenoptera (see pp. 186–7)—have caterpillars (Fig. 70)

with seven or eight pairs of prolegs, the foremost being on the second abdominal segment. The Scorpion-flies and their allies (Mecoptera)—insects sometimes associated with the Neuroptera, but distinguished by their elongate beak-like faces, their predominantly longitudinal wing-nervuration, and the upturned hind abdominal segments of the male with conspicuous genital armature—have as their larvae caterpillars in which the series of prolegs is still more extensive, including possibly nine pairs, which begin on the first abdominal segment; the prolegs of these larvae show indications of jointing. The caterpillars of saw-flies differ from those of moths and butterflies in having no hooks or spines on the prolegs, which attach themselves to the surfaces on which the larva crawls by a sucker-action, the centre of the disc of the proleg being withdrawn from contact so as to enclose a small airless space.

The head of a saw-fly caterpillar has but one simple eye (*ocellus*) on each side instead of the three or four wherewith the moth larva is provided. In many saw-fly caterpillars the head appears small relatively to the body, when compared with that of a beetle grub or the caterpillar of a moth. A tendency to reduction in the larval head-capsule is indeed a marked feature among insects of the order (Hymenoptera) to which saw-flies belong. Female giant saw-flies (or "wood-wasps," *Sirex*) are insects of formidable aspect with the long outstanding ovipositor used for boring timber so as to place their eggs amid food suitable for their larvae. These tree-tunnelling, wood-eating grubs have a soft body with thin, white, flexible cuticle, except that the tail-segment ends in a short, rigid backward-pointing spine. Prolegs are not distinguishable and the thoracic legs are very small, the jointing just defined, but the cuticle feebly chitinized, and the foot segment ending in a soft, blunt tip. The head also is relatively small, its breadth being much less than that of the thorax, so that the larvae offer in this respect a contrast to the soft beetle grubs with legs reduced or wanting described in earlier pages of this chapter (pp. 112–115). The feelers, partly sunk in circular pits, are very small and blunt. The mandibles, adapted for biting wood, are hard and strong; maxillae and labium have rounded lobes beset with fine spines and very short, relatively thick palps. In the allied family of the stem-

saw-flies (*Cephidae*) the thoracic legs of the larva are reduced still further than those of the Sirex grub, being only minute, unjointed processes.

Thus we may pass naturally from these tunnelling grubs with their vestiges of legs to the larvae of the great majority of the Hymenoptera—gall-flies, ichneumon-flies, wasps, bees, ants—in which legs are entirely wanting. A bee grub for example (Fig. 71) has an extremely soft, flexible cuticle, less wrinkled than that of a legless beetle grub, and becomes markedly swollen as, after each moult, it imbibes more and more of the rich food wherewith it is furnished. The head appears disproportionately small in comparison with the body, as the larva increases in size and usually becomes bent on

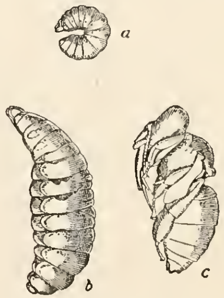



FIG 71. STAGES OF THE HONEY-BEE (*Apis mellifica*).
*a*, young larva; *b*, full-grown larva; *c*, pupa (side views). ×3. After Phillips, *U.S. Dept. Agric.*, *Farmers' Bull.* 447.

itself, with the ventral aspect concave. A peculiarity in the inner structure of these legless hymenopterous grubs is that no waste matter is passed from the food-canal until shortly before pupation, either there is no anus, or there is no connexion between stomach and hind-gut until the last stage of larval life.

The legless type of larva, represented as we have seen among some families of beetles and many sections of the Hymenoptera, is characteristic of the whole order of two-winged flies (Diptera) within which it shows very marked modifications in detail. The structure of the adult Diptera is very highly specialized. The forewings only are developed for flight, the reduced hindwings being modified into small balancing organs (*halters*), and the thorax, dominated as it were by its middle segment,

PLATE I.

Grubs of Black-fly (*Bibio sp.*) feeding in a potato tuber. From *Econ. Proc. R. Dublin Soc.* II.

forms a compact rigid region for the attachment of the strong wing-muscles. The tip of the labium forms a complex sucker, while mandibles and maxillae may be developed as piercers. As our first example from this order, we may take the grub of one of the black-flies (*Bibio*); the stages of *B. johannis*

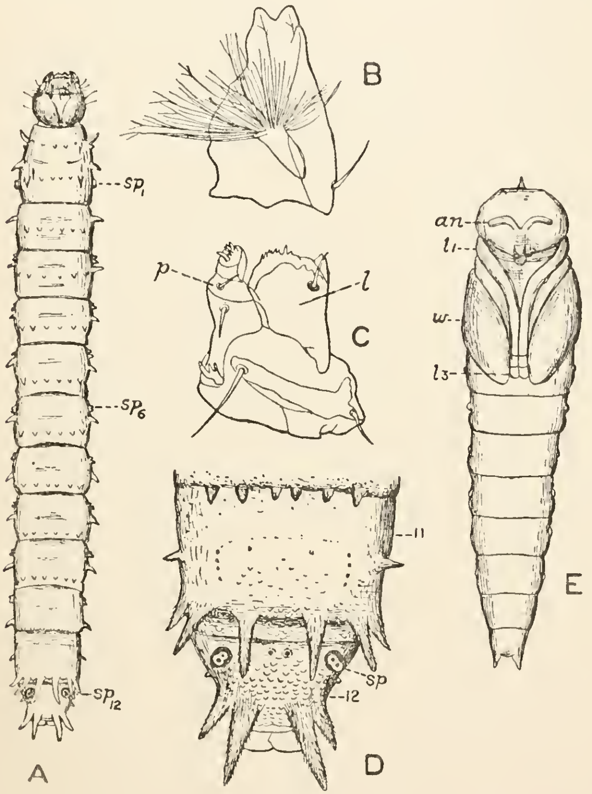



FIG. 72.

A, Larva (dorsal view) of Blackfly (*Bibio johannis*); *sp*, spiracles. × 8. B, mandible, and C, maxilla of larva (*p*, palp; *l*, lobe). × 90. D, terminal segments (11 and 12) of body (*sp*, spiracles). × 20. E, pupa (ventral view); *an*, feeler; *w*, wing; $l_1$, $l_3$, fore- and hind-legs. × 8. After Morris, *Ann. Appl. Biol.* IV.

have been described rather fully.[1] When hatched this larva is about 1.5 mm. long ($\frac{3}{50}$ inch) with a firm rotund head and a body of twelve segments which bear long, slender bristles in

[1] H. M. Morris: "On the Larval and Pupal Stages of Bibio johannis, L.". *Ann. Appl. Biol.*, IV. 1917.

addition to numerous minute spines scattered over the thin, pale cuticle. After two moults the Bibio larva (Fig. 72 A) is fully grown, having reached a length of 10 mm. ($\frac{2}{5}$ inch), the head being of the same rounded shape as before, but relatively shorter and narrower compared with the body. The body-cuticle is tough and brown, drawn out into long conical processes arranged in transverse rows across the segments, and bearing numerous closely-set scale-like spines, many of which have rows of blunt teeth. As in the first stage the body has twelve segments, of which the foremost (prothorax) is much longer than the others and imperfectly divided by a shallow transverse furrow. This larva is remarkable for the number of its spiracles; there are ten pairs of these, a pair on every segment except the mesothorax and the ninth abdominal segment. The spiracles (Fig. 72 A *sp*) stand out laterally from the body on short cylindrical processes, except those of the tail-segment (Fig. 72 D) which are much larger than the others and situated on the dorsal aspect; the spiracles on the prothorax, about half the size of these hindmost, are twice as large as the rest, and it is noteworthy that in the newly-hatched larva only the tail-spiracles are recognizable. Turning to the head-appendages we find that the feelers are very small, the mandible (Fig. 72 B) stout and strong with blunt teeth, the maxilla (Fig. 72 C) with short palp, and broad spinose lobe, and the labium consisting of a jointed plate without definite palps or lobes. At the extreme hinder end of the abdomen two thin-walled conical processes can be protruded by blood pressure; these serve as tail-prolegs. Such "black-fly" grubs live underground, feeding sometimes on decaying organic material and sometimes on fresh plant tissues; they have been found in numbers devouring potato tubers (Plate I). The nervous system of the Bibio larva consists of a brain and sub-œsophageal ganglion in the head, and a ventral chain of three thoracic and eight abdominal ganglia.

Another more familiar root-feeding larva—the "leather-jacket" grub of a crane-fly (or "Daddy-long-legs)" (*Tipula*)[1] —may serve as our next type from among the Diptera. The well-known flies (Fig. 73 *a*) lay their eggs in the soil in summer,

[1] J. Rennie: "On the Biology and Economic Significance of Tipula paludosa". *Ann. Appl. Biol.*, III. 1917.

and the young larvae are hatched about a fortnight later. They have a firm, broad head followed by thirteen body-segments whose cuticle is flexible and wrinkled but tough ; each segment carries on either side a tuft of short bristles ; but at the tail-end the tufts are long and prominent, projecting on either side of the larva. As the grub increases in size through its series of moults it becomes relatively longer in proportion to its breadth, while the bristles appear far less prominent.

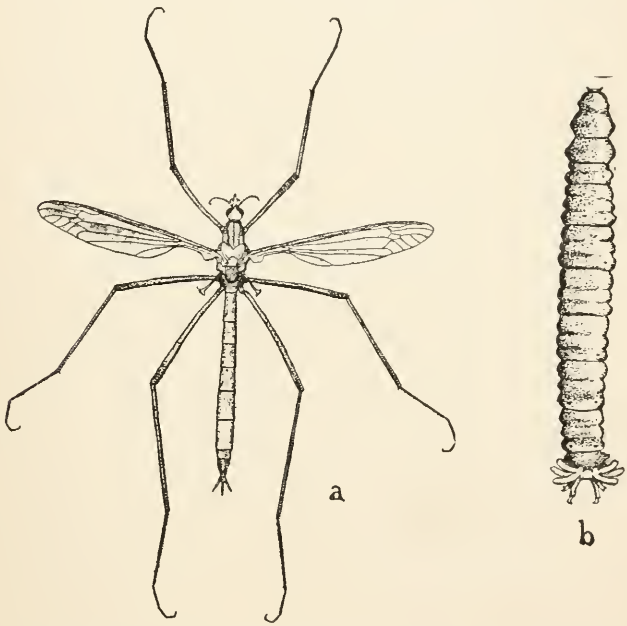



FIG. 73.
*a*, Crane-fly (*Tipula oleracea*) ; *b*, Larva ("leather-jacket" grub) of *Tipula*. × 2. *a*, from Carpenter, "Life Story of Insects" ; *b*, after Comstock, "Introduction to Entomology".

When fully grown (Fig. 73 *b*) the larva of a large crane-fly is about 40mm. ($1\frac{3}{5}$ inches) long, greyish in colour with black spots, the tough cuticle (which has suggested the name of "leather-jackets" for these grubs) strongly wrinkled so that the segmentation is greatly obscured. The best guide for outward distinction of the segments is found in the minute bristles arranged in pairs on the tergal and sternal areas. The head, hard and firm but narrow in proportion to the body, has a pair

of short, stiff, unjointed feelers, and very strong toothed mandibles, adapted for the root-feeding habits of these grubs. The maxillary lobes are also strongly toothed, and in some grubs belonging to this group maxillulae have been detected.[1] A noteworthy feature of the larva is the presence of a strong chitinous plate on either side of the pharynx, strengthening the wall of that organ and affording support to the jaws. Another feature of great importance is the absence of the usual series of lateral spiracles and the restriction of these air-openings to a large pair at the tail-end of the body, somewhat on the dorsal aspect, where they appear as conspicuous circular plates surrounded by outstanding finger-like papillae (Fig. 74). Ventral to this spiracular area is the anus (*A*) surrounded by

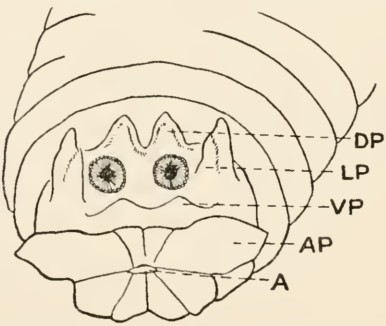



FIG. 74. TAIL-END OF LARVA OF *Tipula paludosa*.
Showing spiracles surrounded by papillae: dorsal (*DP*); lateral (*LP*); ventral (*VP*); *A*, anus; *AP*, anal papilla. × 18. After Rennie, *Ann. Appl. Biol.* III.

lobes, a pair of which, protrusible as "anal prolegs", assist in the locomotion of the grub.

From such grubs we may pass to consider one of the type characteristic of the great majority of the order of the two-winged flies—the *maggot* of a house-fly[2] or a blue-bottle[3] (Fig. 75). Here we find the greatest divergence between the perfect insect and the larva, for the former may perhaps be regarded as the most specialized in structure of all winged insects owing to the high elaboration of some organs and the reduction or disappearance of others, while the latter is not

[1] S. Bengtsson: "Bidrag till Kannedomen an Larven of Phalacrocera replicata". *Act. Reg. Soc. Physiog. Lund. Univ. Arsskr.* XXXIII. 1897.
[2] C. Gordon Hewitt: "The House-fly". Cambridge, 1914.
[3] B. T. Lowne: "The Anatomy, Physiology, Morphology and Development of the Blow-fly". London, 1890-95.

only legless, like many of the larvae hitherto considered, but has no definite head-capsule, so that it represents the extreme of specialized degradation. The cuticle, soft and flexible, allows the internal white fatty tissue to show through, so that the maggot presents a pale creamy appearance. Its form is tapering, the front end being narrow and the tail broad (Fig. 75, *a*, *b*). The mouth opens at the extremity of the cylindrical anterior region which can be protruded and withdrawn as the larva moves and feeds. Just above the mouth a pair of little

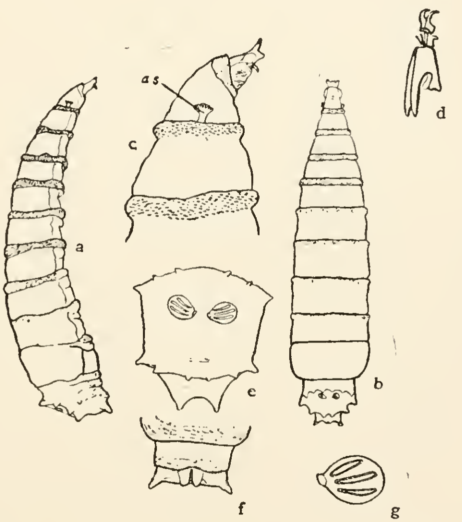



FIG. 75. MAGGOT OF GREENBOTTLE FLY (*Lucilia sericata*). *a*, side view; *b*, dorsal view. ×4. *c*, front end (side view) (*as*, anterior spiracle); *d*, mouth-hooks (side view); *e*, tail-region, dorsal aspect; *f*, tail region, ventral aspect, with anal prolegs protracted. × 10. *g*, right tail-spiracle. × 20. After Carpenter, *Econ. Proc. R. Dublin Soc.* I.

sensory processes are situated, and from the mouth-opening project the extremities of a pair of sharp, curved mouth-hooks (Fig. 75, *c d*) which serve the maggot for tearing up its food. These hooks are jointed to short, stout *hypostomial sclerites* which at their hinder ends articulate with the large winged *pharyngeal sclerites* on either side of the pharynx. Behind the narrow mouth-bearing region eleven body-segments can be distinguished, increasing in size towards the tail-end. Most of these have rather prominently outstanding ridges on

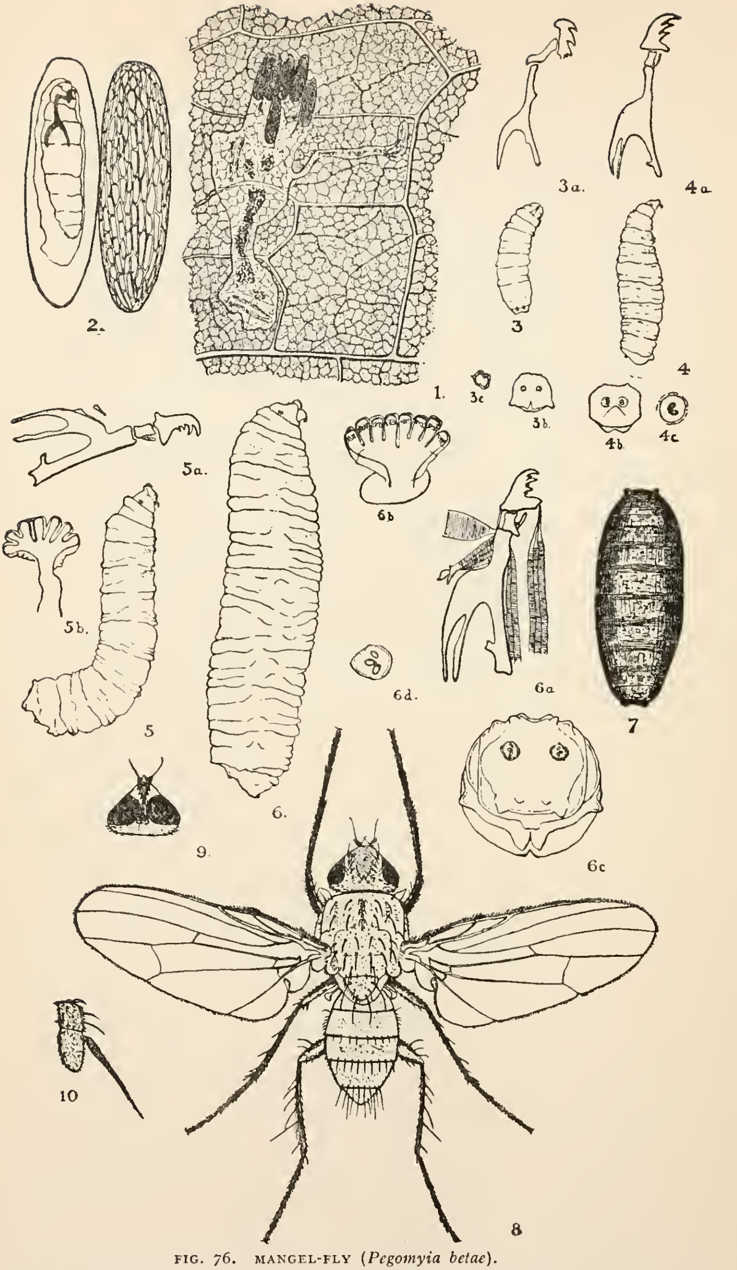



FIG. 76. MANGEL-FLY (*Pegomyia betae*).

1. Portion of leaf with cluster of eggs and burrows formed by young maggots. × 7. 2, two eggs, one showing external sculpture, the other a ripe embryo surrounded by membrane. × 35. 3, newly-hatched maggot; 4, second-stage maggot. × 12. (3*a*, mouth-hooks. × 75; 4*a*. mouth-hooks. ×54. 3*b*, 4*b*, tail-ends of 3 and 4. × 30. 3*c*, 4*c*, tail-spiracles of 3 and 4. × 75); 5, late maggot. × 7. (5*a*, mouth-hooks. × 35. 5*b*, front spiracle. ×130); 6, full-grown maggot. × 7 (6*a*, mouth-hooks with muscles. × 35. 6*b*, front spiracle. × 130. 6*c*, tail-end of maggot. ×14. 6*d*, tail-spiracle. ×45). 7, puparium. × 7. 8, female fly; 9, head of male. × 7. 10, feeler of male. × 30. From Carpenter, *Econ. Proc. R. Dublin Soc.* I.

the ventral aspect, beset with numerous fine bristles which assist the maggot's crawling action.

A flattened dorsal area (Fig. 75, *g*) of the hindmost segment slopes steeply backwards and, like the corresponding region in the crane-fly grub, carries the pair of large tail-spiracles. These are circular in outline, each with three narrow slits through which air passes in and out of the breathing tubes. From these tail-spiracles the main air-trunks run forward along the sides of the body, becoming narrower towards the head-region and terminating in a pair of small anterior spiracles (Figs, 75 *c*, 76 6*b*) situated at the sides of the first body-segment behind the anterior mouth-bearing region. These spiracles, minute and apparently of little functional importance, are remarkable in their form ; the front end of the air trunk divides into eight or ten little tubes divergent but remaining in contact with each other, the whole structure showing as a beautiful little fan-like object against the white surface of the larva. In connexion with the extreme reduction in the number of spiracles among these fly larvae it is of great interest to notice that in a few muscoid maggots[1] a series of five or six pairs of vestigial abdominal spiracles has been detected, these minute openings in the cuticle being connected with the tracheal system by air-tubes which become solidified by the filling up of their cavities (Fig. 77). As in the crane-fly's grub, the spiracular area on the blow-fly maggot's tail-segment is surrounded by regularly arranged, conical, finger-like processes, and the somewhat ventrally situated anus has a blunt " proleg " on either side. In the successive stages of such a maggot the mouth-hooks and the tail-spiracles show an advance in the complexity of their structure (Fig. 76).

This fly-maggot is so important a type of insect larva that a brief account of its internal structure, such as has been given in some previous cases, seems desirable. In the digestive system, the pharynx with its chitinized lateral walls is succeeded by a tubular gullet (Fig. 78 *oe*) from the forward region of which is given off a bladder-like sucking sac. The gullet expands into a small crop (*c*), the hindmost portion of

[1] L. C. Miall and T. H. Taylor : " The Structure and Life History of the Holly-fly ". *Trans. Entom. Soc., Lond.* 1907. G. H. Carpenter and F. J. Pollard : " The Presence of Lateral Spiracles in the Larva of Hypoderma ". *Proc. R. Irish Acad.*, XXXIV. 1917.

the fore-gut. The stomach (Fig. 78 *s*)—lined with digestive cells uncovered by cuticle—is a coiled tube somewhat broader than the gullet ; it gives off four short, blind tubes at its front end, immediately behind the crop. Behind the stomach

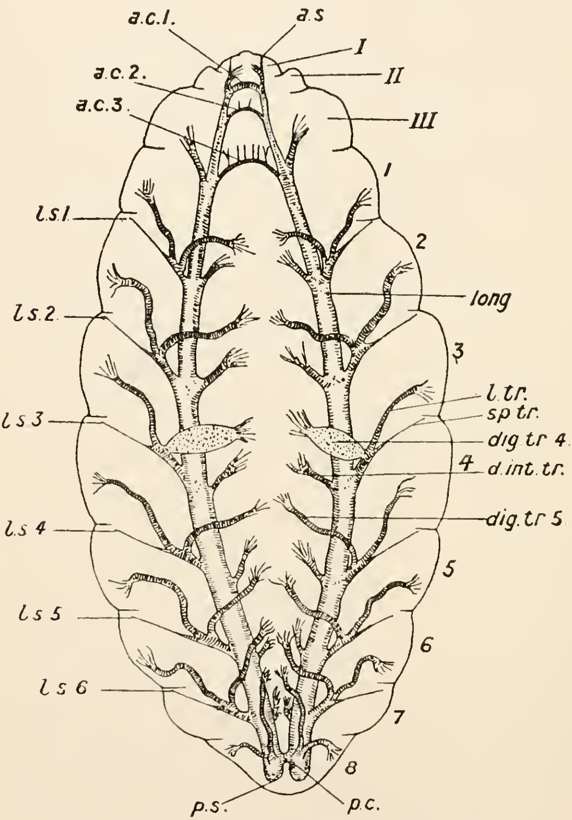



FIG 77. FULL-GROWN LARVA OF OX WARBLE-FLY (*Hypoderma bovis*). DIAGRAM OF TRACHEAL SYSTEM. ×5.

*I—III*, segments of thorax ; 1—8, segments of abdomen ; *a.s*, anterior spiracles ; *l.s.*1—6, lateral spiracles ; *p.s.*, posterior spiracles ; *long.*, longitudinal tracheal trunks ; *a.c.*, 1—3, anterior connectives ; *p.c.*, posterior connective ; *d.int.tr*, dorsal internal tracheae ; *dig. tr.*, tracheae to digestive tube (numbers refer to the abdominal segments ; note the sac-like swelling of *dig. tr* 4) ; *l.tr.*, outer lateral tracheae ; *sp. tr.*, spiracular tracheae (solidified). From Carpenter and Pollard, *Proc. R. Irish Acad.* XXXIV.

comes the narrower hind-gut or intestine (Fig. 78 *int*) derived from the posterior ectodermal ingrowth and lined with chitin, at its junction with the stomach come off paired Malpighian

or excretory tubes, each of which a very short distance from its origin divides into two, so that the maggot has four of these tubes, the same number as the fly.

The nervous system of the maggot shows a most remarkable

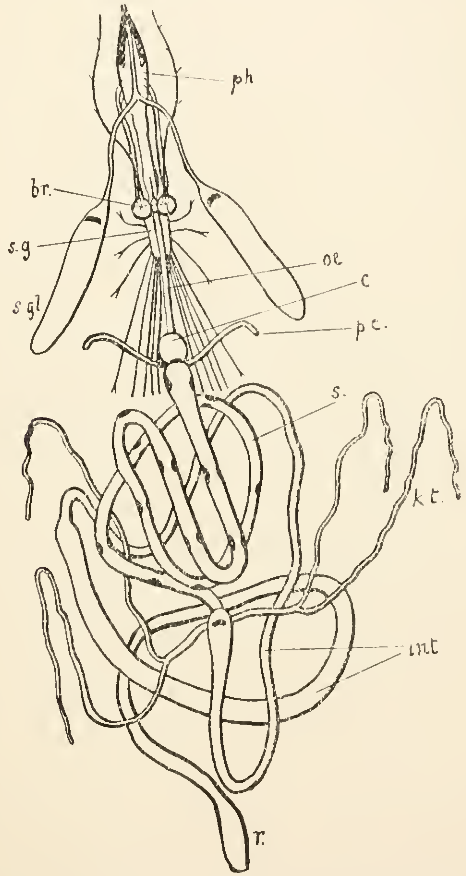



FIG. 78 DIAGRAM OF THE NERVOUS AND DIGESTIVE SYSTEM OF A MUSCOID MAGGOT.

*br*, brain: *s.g.*, ventral ganglion with diverging nerves; *ph*, pharynx; *oe*, gullet; *c*, crop; *s.gl*, salivary glands; *pc*, pyloric caeca; *s*, stomach; *kt*, kidney tubes; *int*, intestine; *r*, rectum. Position of imaginal groups of cells shown by black patches. ×10. Adapted in part from Lowne and Hewitt.

concentration. The brain (Fig. 78 *br*), consisting of a pair of compound ganglia, lies above the gullet some distance back from the mouth in the thoracic region of the larva. Immediately

behind the brain and beneath the gullet is a large, elongate nerve-centre, representing the whole chain of ventral ganglia fused together, paired nerves radiating from it to the various segments of the larva. This highly-specialized concentration of the nervous system shows a marked contrast to the typical, segmental arrangement in the Bibio larva described above (p. 128).

The series of insect larvae mentioned in this chapter illustrate, it will be seen, an increasing divergence between the form of the creature in its final winged condition and in its preparatory state. The grub of the ground-beetle (see p. 100) with its large, firm head-capsule, well-armoured body, and long legs with two-clawed feet, differs far less from its parent than the soft, degenerately modified, headless and legless maggot, that we have just been considering, differs from the fly. The importance of this graded array of larvae with their varying characters has been recognized by all students of insect transformations, though greatly divergent views have been held as to the interpretation of the fact. At this stage of our discussion of the subject it may suffice to call attention to two points. The greatest difference between imago and larva is shown among those insects that are most highly specialized structurally. And where—as in the case of the oil beetles and Mantispa—two or more larval forms occur in the same life-history, the active armoured larva precedes the soft, legless grub in order of appearance.

### B. DIFFERENCES AMONG PUPAE

Among those insects whose wing-growth is of the hidden or inward type, the pupa is a most characteristic stage in the life-history. Its usually quiescent habit gives opportunity for the transition from larva to imago. While less absorbing as an object of study than the larva that precedes or the imago that follows it, the pupa has many features of interest worthy of attention.

We have seen that the wings of insects of the group under consideration become apparent at the pupal stage. Among beetles (Fig. 56, *f*), lacewing-flies (Fig. 68 *e*), caddis-flies, wasps and bees (Fig, 71 *c*), the pupal wings, as well as the

feelers, legs and other appendages, stand out from the body much as they do in the perfect insect. Such pupae are defined as *free*. But among butterflies (Fig. 33) and the great majority of moths, the wings and other appendages have their cuticle coherent with that of the body generally, so that these do not stand out distinctly but appear to be fixed to the thorax and abdomen. Such a pupa is said to be *obtect*.

In the transformations of any insect, the pupa with its visible wings resembles the perfect insect more closely than it

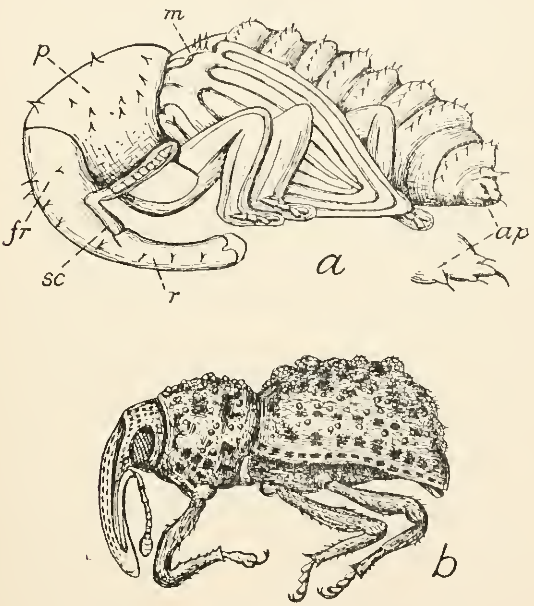



FIG. 79. AUSTRALIAN WEEVIL (*Syagrius intrudens*).
*a*, lateral view of pupa. × 12. (*fr*, frons; *r*, rostrum; *sc*, scape of feeler; *p*, prothorax; *m*, mesothorax; *ap*, anal process: this shown below. × 30); *b*, Lateral view of imago. × 7. After Mangan, *Journ. Econ. Biol.* III.

resembles the larva. If the *free pupae* of a series of beetles be observed and each compared with its respective imago, it will be found to display some distinctive feature of its family or genus. Thus we find that after the final moult of a wire-worm (see p. 108), when the pupa[1] is revealed (Fig. 60 *h*) its

[1] G. H. Ford: "Observations on the Larval and Pupal Stages of Agriotes obscurus". *Ann. Appl. Biol.*, Vol. III. 1917.

prothorax has the hind corners projecting as sharp points like those of the adult click-beetle. So the pupa of a weevil,[1] succeeding the soft, legless grub already described in this chapter, has the prolonged snout and elbowed feelers that distinguish the head in beetles of its family, and the shape and relative length of this characteristic snout would often enable an entomologist to determine the tribe or genus to which a particular weevil pupa should be referred (Fig. 79). In beetle pupae generally, however, it is to be noted that the prothorax and head are strongly flexed ventralwards, and that feelers, jaws, and legs usually lie directed backwards along the ventral aspect of the insect. While the wings in the perfect beetle lie over the back, the forewings or elytra reaching often to the hinder end of the abdomen, the wings of the pupa are lateral or ventro-lateral in position, and very much shorter than those of the beetle, the tips of the elytra being opposite the middle abdominal region. In this respect, therefore, the pupal wings correspond in the degree of their development with the wing-rudiments of the advanced nymph in an exopterygote life-history. The same pupal type is found in the transformations of the various families of lacewing-flies and allied insects (Neuroptera). For example the Australian Psychopsis, the larva of which has been described in this chapter (*supra*, p. 119), has a pupa (Fig. 68 *e*) " closely resembling the imago in everything except its unexpanded wings ".

In the *obtect pupa* of a moth or butterfly (Fig. 33) the adhesion of the wings and appendages to the body masks the correspondence of the creature in this stage with the perfect insect, suggesting the fanciful likeness to a swaddled infant that first led to the use of the term *pupa* in entomology. In such a pupa, the outline of the forewing can be clearly traced, the costa being ventro-lateral in position, as in a " free pupa," but glued as it were to the body-cuticle, the feeler lying close against the costa on either side, and the maxillae and legs being visible between the feelers ventrally; these various organs stand out as ridges on the general surface. The hinder half of the abdomen projects beyond the tips of the pupal wings, and, as already briefly mentioned in a previous chapter

[1] J. Mangan: " The Life-history of Syagrius intrudens ". *Journ. Econ. iol.*, Vol. III. 1908.

(p. 63) a specialized dorsal tail-region (or *cremaster*) (Fig. 33 *cr*) armed with hook-like spines serves to fasten the pupa to its silken cocoon or suspensory pad.[1] This cremaster is a modification of the caterpillar's spiny *suranal plate*, lying dorsal to the intestinal opening. After liberation from the larval cuticle this cremaster is worked into the silken meshes so that the pupa is safely anchored ; in the case of those butterfly pupae which hang head downwards from a pad of silk—those

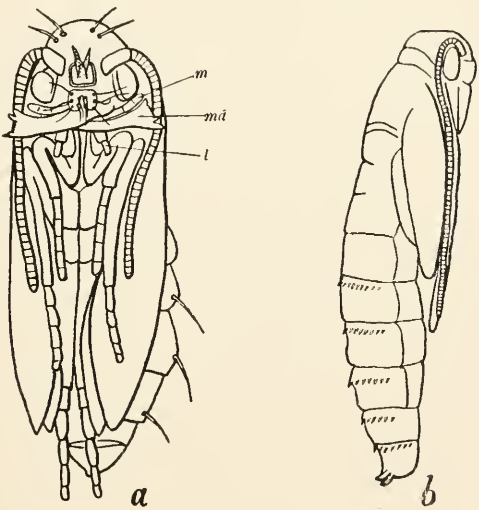



FIG. 80.
*a*, " Free " Pupa of primitive Moth (*Eriocrania*), ventral view ; (*md*, mandible ; *m*, maxillary and *l*, labial palp). × 10. After Packard, *Mem. Nat. Acad. Sci.* VII. *b*, " Incomplete " Pupa of clothes moth (*Tinea*), side view. × 8. In part after Packard.

of the brightly-coloured " Red Admiral," " Peacock," and other of our native vanessids for example—the cremaster thus becomes an essential means of support.

Some interesting transitional conditions between the typical free and obtect pupæ can be observed among insects of various groups. Thus in the pupa of some two-winged flies (Diptera), while the head-appendages and wings are adherent to the body, the legs are free. Moths of the more primitive families

[1] W. Hatchett Jackson : " Morphology of the Lepidoptera ". *Trans. Linn. Soc. Zool.* (2), Vol. V., 1890. E. B. Poulton : " External Morphology of the Lepidopterous Pupa ". *T. c.* 1898.

have pupae with the appendages and wings less closely adherent than those of the more specialized Lepidoptera; such pupae are often defined as "incompletely obtect" or *incomplete.* While an obtect lepidopterous pupa has usually only two or three abdominal intersegmental junctions with flexible cuticle, so as to allow freedom of movement between very few abdominal segments, an "incomplete" pupa (Fig. 80) may have four or five segments capable of movement.[1] The abdominal segments in an "incomplete" pupa are often provided with rows of spines, which are not present on an obtect pupa. This difference is correlated with a divergence in behaviour, for the spines are serviceable to the former in facilitating its partial emergence from the cocoon in preparation

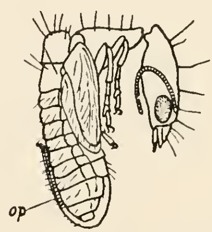



FIG. 81. PUPA OF FEMALE SNAKE-FLY (*Raphidia*), SIDE VIEW. *op*, ovipositor. × 3.

for the final moult and the liberation of the imago, while the latter, which has no spines, remains enclosed in its cocoon or attached to its suspensory pad, so that all necessary locomotion must be performed by the winged adult after the final moult.

Such differences among pupae as regards activity and power of locomotion are often associated with peculiar modes of life as well as with characteristic structural features. It may suffice to mention the case of the curious snake-flies (*Raphidia*), of which the pupa (Fig. 81) is easily recognized as it presents the distinctive narrow, elongate head and prothorax of the imago. For the greater part of its life as a pupa it remains at rest in a cavity of the wood which served the larva as a hunting ground, but as the time for the final moult draws near it leaves its shelter and runs about actively.

[1] T. A. Chapman: "Structure of Pupae of Heterocerous Lepidoptera". *Trans. Entom. Soc., Lond.* 1893.

The pupal stage of the caddis-flies[1] (Trichoptera) is also noteworthy, exhibiting special adaptations to life under water. It has been mentioned (p. 122) that the larvae of these insects live in cases or " houses ", composed of fragments of vegetable matter or small stones fastened together by silken threads,

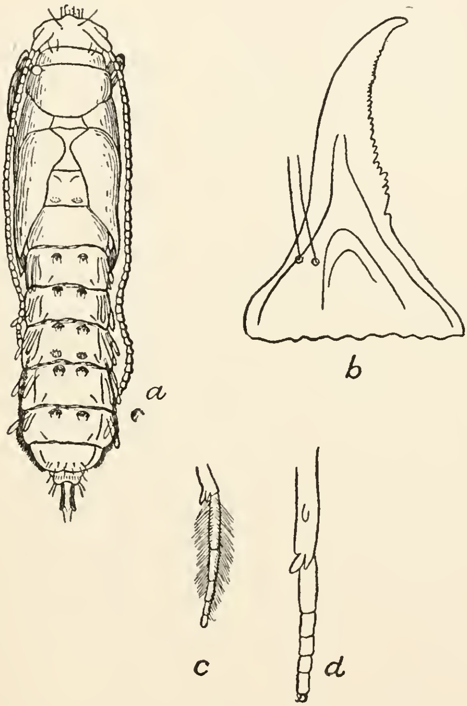



FIG. 82.
Pupa of Caddis-fly (*Stenophylax*), dorsal view. × 8. *b*, mandible of caddis-pupa (*Sericostoma*). × 50. *c*, fringed foot of caddis-pupa (*Potamorites*). × 6. *d*, clawed foot of caddis-pupa (*Ptilicolepus*). × 24. After Thienemann, *Biologie der Trichopteren-Puppe.*

and that they breathe by means of tubular gills. Before pupation the larva shortens its case and constructs a wall at the end formerly open, leaving, however, apertures for the passage of water-currents which bathe the gills situated in series on the abdominal segments ; and it is of importance

[1] A. Thienemann : " Biologie der Trichopteren-Puppe ". *Inaug. Dissert. Greifswald.* Jena, 1905.

that throughout pupal life these organs should be kept in constant motion. The caddis-pupa (Fig. 82) has, like the larva, strong biting mandibles, though these appendages are wanting or vestigial in the imago. They are required in order that the pupa may bite its way out of the case, so as to rise through the water into the atmosphere before the emergence of the fly. This upward passage through the water is in some cases performed by crawling, and in others by swimming, as the legs of various caddis-pupae are provided either with claws for clinging to the stems and leaves of aquatic plants, or with rows of delicate swimming hairs, which facilitate free locomotion in the pond or stream (Fig. 82 *c, d.*)

Reference has been frequently made to the *cocoon* or protective case which surrounds the pupa. In the life-history of the caddis-flies, just now under consideration, the "house" of the larva, shortened and closed, becomes the shelter of the pupa, and this is built of surrounding objects or fragments spun together by the silk that the larva secretes from the long tubular glands which open into its mouth (see p. 122 above). There are many other insect life-histories in which the pupal cocoon may be regarded as the modification of a larval shelter, and always the cocoon is the result of the larva's work before the final moult, its spinning activity being a preparation for the pupal life. A moth-caterpillar, for example, that has completed its growth from hatching, feeding uncovered on the leaves of plants, surrounds itself with a cocoon (Fig. 83) that has relation not to the needs of its own stage in the transformation but to those of the next.

Many pupae are found buried in the soil; such may be protected by a cocoon of fragments of earth fastened together by silk, or the earthen chamber may have a silken lining. The "Goat" caterpillar (*Cossus*) after its long period of feeding in the wood of trees constructs a cocoon of chips and splinters, while many cocoons are strengthened by the shed hairs or spines of the caterpillar or by some hardened solidified secretion. On the other hand the cocoon may be formed entirely of silk as in the well-known work of the "Silkworm" (*Bombyx*). Such a silken cocoon may be, as in this case, dense and extensive, composed of a comparatively enormous length of thread, or it may be loose and scanty, a mere network

as the cocoon of the small turnip-eating caterpillar (*Plutella maculipennis*). The pupa of a white butterfly (*Pieris*, Fig. 33), or a Swallow-tail (*Papilio*) has the cocoon reduced to a pad of silk to which the cremaster is anchored, and a supporting girdle-thread around the thorax. Among the brilliant vanessid butterflies the pupa is without this latter remnant, and hangs head downwards from the silken tail-pad which alone represents the cocoon.

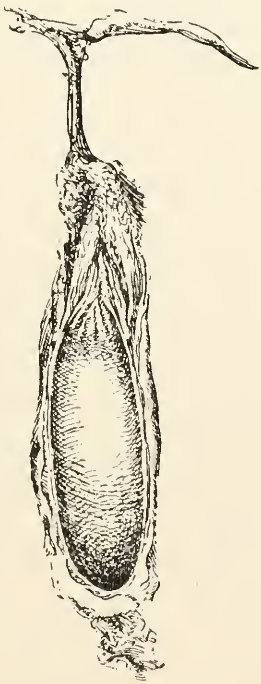


FIG. 83. COCOON OF SILK MOTH (*Callosamia promethea*) IN LONGITUDINAL SECTION. Natural size. After Comstock, " Introduction to Entomology ".

A remarkable structure for the protection of the pupa, is the *puparium*, characteristic of many families among the Diptera or two-winged flies, especially such as the blue-bottle group whose larva is a maggot. This puparium (Fig. 76, 7) is the hardened and modified larval cuticle, which, after separation from the underlying tissue is not shed, in accordance with the usual process at pupation, but becoming firm in

texture, usually dark in colour and shortened, forms a more or less rigid protective case, enclosing the pupa whose cuticle is thin and delicate. Distinctive features of the maggot, such as the arrangement of the spines on the segments and

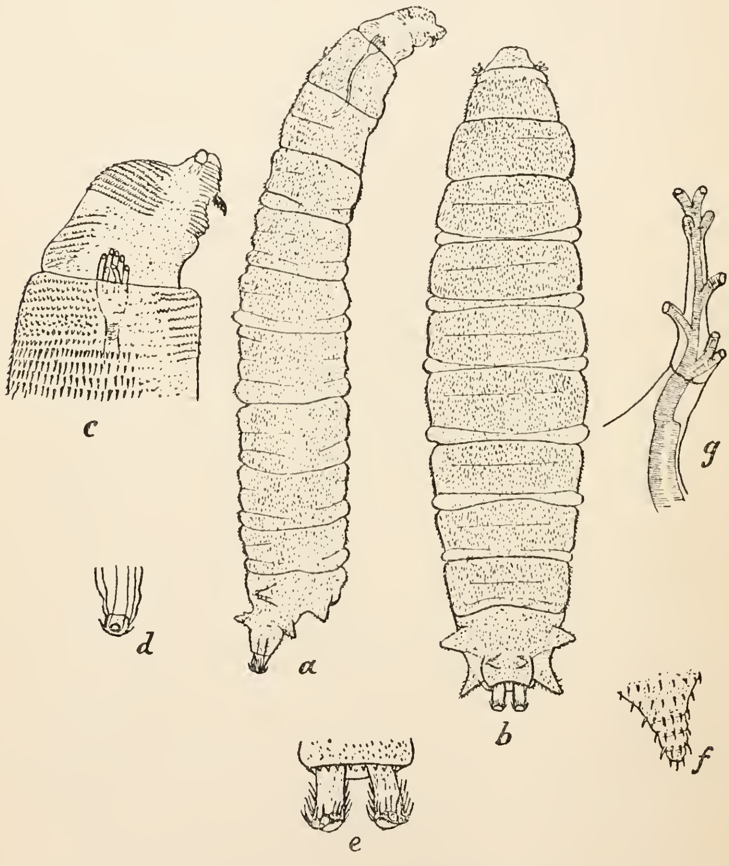



FIG. 84. LEAF-MINING MAGGOT OF *Scaptomyza flaveola*.
*a*, lateral view; *b*, dorsal view. ×30. *c*, front end, showing mouth-hooks, anterior spiracles, and armature of cuticle; *d*, *e*, tail-spiracles (lateral and dorsal views); *f*, tail-process. × 80. *g*, Anterior spiracle of Puparium. ×120. From Carpenter, *Econ. Proc. R. Dublin Soc.* II.

the form of the spiracles (Fig. 84) can often be clearly recognized on the puparium. It is noteworthy that the tail-spiracles on which the maggot depends for its air-supply are closed in the puparium, the functional spiracles, connected with the

air-tubes of the enclosed pupa, being placed far forwards, often on prominent processes (Fig. 84 *g*). A sub-circular lid at the front dorsal region of the puparium often breaks away neatly to allow the fly when developed to escape, and the *suture* or surrounding margin of this—a narrow depression along which the cuticle is thin and weak—can in some cases be seen in the cuticle of the final larval stage, affording an interesting example of a specialized provision preformed for the needs of the latest stages of the insect's development.

### (c) SOME FEATURES OF INTERNAL CHANGE

The transitions from larva to pupa and from pupa to imago in the insect life-histories sketched in the preceding pages, are necessarily accompanied by marked changes in the outward form. The cuticular envelope is remade at every stage of the life-cycle even if, as in the successive instars of a beetle grub, caterpillar, or maggot, no conspicuous transformation be apparent; and at what may be regarded as the crises of transformation—pupation and final emergence—the change revealed is often startling in its extent. Some reference has already been made (pp. 63–4), to the inward modifications which accompany these outward changes, and it should be clear that while some larval systems grow directly into the corresponding structures of the imago, others are broken down during the pupal stage, and the corresponding parts of the perfect insect are at the same period built up from the minute imaginal discs of the larva.

Among the organs that grow continuously through the stages of the life-history, the essential reproductive structures are especially typical. The germ-cells of an insect are recognizable in the early embryo. In a leaf-beetle (*Cyltia*) they are differentiated from the newly-formed blastoderm.[1] In a common midge (*Chironomus*) two conspicuous cells which are the primordial germs can be seen even before the formation of the blastoderm.[2] From these are derived the ovaries or testes of the female or the male respectively, the cells multiplying

[1] A. Lécaillon: "Récherches sur l'Oeuf et sur le Developpement de quelques Chrysomelides". *Arch. d'Anat. Microsc.*, II. 1898.

[2] E. G. Balbiani: "Contribution â l'Étude de la formation des Organes Sexuels chez les Insectes". *Rec. Suisse Zool.*, II. 1885.

through the period of embryonic growth[1] and the organs, sexually differentiated, being visible through the transparent body-wall of the aquatic larva or "blood-worm", in the later stages of which the genital ducts also may be seen.[2] These latter arise in moths and butterflies from strands of tissue, known as the genital cords, connecting the testes or ovaries with the ventral body-wall. External reproductive structures, however, such as the ovipositor as well as the terminal median chitin-lined tube—the vagina of the female or the ejaculatory duct of the male—are present in the larva only as inwardly-growing imaginal buds,[3] which during the pupal stage become developed into the adult condition. Meanwhile by the multiplication and modification of germ-cells the rudimentary ovary shows increasing differentiation of the ovarian tubes, with their delicate epithelial walls and contained eggs, while the testis also grows rapidly, its cavity becoming lobulated, and the contained immature male germ-cells (*spermatogonia*) dividing so as to give rise ultimately to the active mobile sperm-cells (*spermatozoa*). Thus, quickly after emergence from the pupal cuticle, the winged adult insect may be ready for the breeding function.

At this point it may be well to mention some very curious cases of abnormal hastening of the development of the eggs in certain insects which become capable of reproduction before they have completed their transformations. The midge Chironomus has just been mentioned, and in one species, at any rate, it was observed fifty years ago[4] that the female pupa may lay eggs which, without fertilization develop into larvae. This may clearly be regarded as a case of precocious virgin reproduction (parthenogenesis), and we have seen that egg-laying or the birth of active young from virgin females is a common feature in the life-cycle of most kinds of greenfly (*Aphididae*). It had previously been noticed[5] that among

[1] R. Ritter: "Die Entwicklung der Geschlechtsorgane und des Darmes bei Chironomus". *Zeitschr. f. wissensch. Zool.* LI. 1890.

[2] L. C. Miall and A. R. Hammond: "The Structure and Life-history of the Harlequin Fly". Oxford, 1900.

[3] W. Hatchett Jackson: "Studies in the Morphology of the Lepidoptera". *Trans. Linn. Soc.*, Vol. V. 1890.

[4] O. Grimm: "Die ungeschlechtliche Fortpflanzung einen Chironomus" *Mem. Acad. St. Petersburg* (7), XV. 1870.

[5] N. Wagner: "Ueber die viviparen Gallmückenlarven". *Zeitsch. f. wissensch. Zool.*, XV. 1865.

certain members of the gall-midge family (*Cecidomyidae*), larvae might contain within their bodies small live larvae which ultimately made their way out through the skin and cuticle of their precocious parent, and later it was seen[1] that these offspring arise from eggs, which breaking loose from the early-developed ovaries, float about in the body-cavity where they undergo segmentation and growth. After several of these abnormal generations the larvae are stated to pupate and develop into male and female midges. Such power of reproduction by immature creatures (*paedogenesis*) though very remarkable and interesting, is not unknown among other groups of animals, in some cases as a normal phase in the life-history.

The central nervous system commonly passes like the reproductive organs from the larval through the pupal to the perfect stage by a gradual process of growth and change without sudden and critical transformation or re-making.[2] From the brief account already given (ch. ii, pp. 56, 60) of the nervous system of a butterfly as compared with that of its caterpillar, it may be inferred that the three thoracic ganglia, spaced from one another in the larva become closely approximated in the imago, while the number of abdominal ganglia becomes reduced through the coalescence of the hinder two or three. Such concentration in the adult as compared with the larva is shown still more markedly in the case of a bee, whose grub has three distinct thoracic and eight abdominal ganglia, while in the winged insect the thoracic ganglia are closely coalesced and there are only five abdominal. On the other hand there are larvae, such as the maggot of a blue-bottle, in which, as already mentioned (p. 136), all the nerve-centres behind the brain are combined in a large mass lying below the gullet. In the adult blue-bottle the same concentration is maintained, but the ventral ganglion now lies in the thorax some distance behind the brain and a median cord extends backwards into the abdomen. It is particularly interesting to find some flies

[1] M. Ganin : " Neue Beobachtungen über die Fortpflanzung der viviparen Dipterenlarven " . *Zeitsch, f. wissensch Zool.* XV. 1865. W. Kahle : " Die Paedogenesis der Cecidomyiden " . *Zoologica*, IV. 1908.

[2] G. Newport : " On the Nervous System of the Sphinx ligustri ". *Phil. Trans. R. Soc.* 1832-4. And " Insects ", in Todd's " Cyclopædia of Anatomy," Vol. II. 1839.

whose larvae have the nervous system concentrated like that of the blow-fly maggot, but which in the adult state possess from two to five distinct abdominal ganglia though the thoracic nerve-centres are all combined. Certain members of the family *Stratiomyidae*, and of the *Syrphidae*: the wasp-like *Volucellae*[1] for example, afford examples of this curious modification in which it is clear that the nervous system of the larva has undergone a greater specialization from the primitive segmented type than has that of the imago. A feature common to all these transformations of the nervous system is the rapid growth of the brain both in size and complexity during the early pupal period, so as to bring about the correlation of that great nerve-centre with the highly organized head of the adult with its elaborated sense-organs.

Turning to the circulatory system, it appears that the heart, a comparatively simple tubular organ in both larva and adult, survives with modifications all the stages of the life-history,[2] continuing its rhythmical contractions during the pupal period. Part of the pericardial tissue also persists from the larva to the imago.

The digestive system of a transforming insect undergoes on the other hand an extensive process of destruction and rebuilding, especially in cases where the manner of feeding of the larva differs markedly from that of the adult. Attention has already been drawn, for example, to the striking contrast between the food-canal in caterpillar and butterfly (pp. 59–60, Fig. 30), adapted respectively to the digestion of solid and liquid food. The lining of the larval stomach undergoes degeneration and the cells are shed into the cavity, while from small deeply-situated replacing cells the more delicate lining of the adult stomach is developed. This process has been lately studied in the development of bees and wasps[3] in whose grubs the replacing cells can be already distinguished in sections through the stomach taken at an early larval stage (Fig. 85). It has been previously mentioned that the greater portion of

[1] J. Künckel d'Herculais: "Récherches sur l'organization et le développement des Volucelles". Paris, 1882.

[2] A. Kowalevsky: "Die nachembryonale Entwicklung der Musciden". *Zeitsch. f. wissensch, Zool.*, XLV. 1887.

[3] J. Anglas: "Observations sur les Métamorphoses internes de la Guêpe et de la l'Abeille." *Bull. Sci. France et Belg.*, XXXIV. 1901.

the digestive tract in many insects is formed from a forward and a hinder inpushing of the outer skin lined with chitinous cuticle. This cuticle is, of course, shed at the crisis of transformation, and the cellular layer (*epithelium*) is broken down in order that a new fore- and hind-gut, adapted to the needs of the adult, may be formed from special bands of cells which surround the food-canal at the hinder end of the proventriculus and at the front end of the intestine (Fig. 78). The salivary glands opening into the mouth also undergo destruction and rebuilding but the excretory (Malpighian) tubes, given off at the front end of the intestine, survive from the larval to the adult state with comparatively slight change.

Muscular tissue forms a large proportion of the mass of an

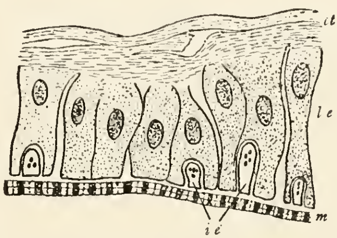



FIG. 85. SECTION THROUGH WALL OF INTESTINE OF LARVA OF WASP (*Vespa*).

*ct*, chitinous lining ; *le*, larval epithelium ; *m*, muscular coat ; *ie*, small cells of imaginal epithelium. After Anglas, *Bull. Sci. France et Belg.*, XXXIV.

insect's body both in larval and adult life ; movement of the segments of body and limbs on one another, of the wings and of the digestive tube, is always due to the contraction of bundles or sheets of muscle fibres. The arrangement of many of these muscles necessarily differs in larva and imago respectively on account of the difference in the body-form, and consequently much of the larval muscular system is broken down during the pupal stage, while the most important muscles of the winged adult are then built up from special groups of imaginal cells.

In an insect larva there is usually much fat distributed in masses of cells in the walls and cavity of the pericardial blood-space and in the great blood-space surrounding the digestive and other organs. These fat-cells form a reserve of

food material. In the adult insect the fatty tissue is less extensive, a very large proportion of the larval fat is therefore absorbed during the pupal period and some of its transformed substance may go to supply the material needed for other tissues.

The breaking-down (or histolysis) of the various larval structures is believed to be due, in great measure, to the activity of special cells—the *phagocytes*—which, like the white blood-corpuscles of vertebrates, have the power of ingesting the cells destined for dissolution. In many cases, however, internal chemical changes within the doomed cells themselves are believed to be the cause of the destructive process, and the activity of the phagocytes will then be displayed in devouring the products of disintegration.[1] A feature of much interest in the microscopic structure of transforming insects is the small size of the cells of various tissues in the winged adult, compared with their comparatively large size in the corresponding tissues of the larva. This contrast (Fig. 85) is particularly noticeable in the remarkable cells known as *oenocytes*—of relatively great size in insect larvae—which are found in close association with the fatty tissue of the blood-spaces and the finest branches of the air-tube system (Fig. 11 *oe*), and are believed to be concerned in the functions of metabolism and excretion.

The air-tubes of an insect are derived, as previously mentioned (p. 19), from inpushings of the skin or ectoderm and are lined with a sheet of chitin continuous with the outer cuticle, shed like the latter at every moult. But at the pupal stage the change in the respiratory system is much more profound than this ; much reconstruction of the cellular wall of the tracheal tubes is then effected, because the breathing organs of a flying insect must needs differ in many respects from those suited to a crawling larva, while in the case of larvae living in water special modes of breathing must be adapted to the aquatic life. In a fly-maggot there are but two effectively acting spiracles at the tail end, whereas in the pupal stage the prothoracic spiracles alone are functional, and in the winged insect there may be six laterally-situated pairs. Hence much of the larval tracheal system must be

[1] *See* L. F. Henneguy's " Les Insectes ". Paris, 1904. (pp. 677-687).

broken down by histolysis, and new regions arise from groups of imaginal cells. The degree of replacement necessary increases with the increase of divergence between imago and larva. In wasps and bees the cellular walls of the main air-trunks pass over from the grub to the adult with considerable increase in capacity brought about by the multiplication of cells, and even in the transformation of the maggot into the blue-bottle the great bladder-like tracheal enlargements known as air-sacs have a similar relation to the larval condition. The excessively fine tubular terminations of the respiratory system, which are known as tracheoles and have no spiral thickening to their chitinous wall, the product of intracellular activity of the living tracheal epithelial layer, become greatly multiplied in preparation for the increased oxidation necessary during the aerial life of the adult, for it is through the exquisitely delicate walls of these tracheoles that the gaseous exchanges between the air and the tissues are carried on.

From the system of air-tubes with their cuticular lining we pass naturally to consider a few special features in the origin of the outer cuticular structures of the adult in relation to the groups of living cells through whose activity they are formed. It has already been explained how in metamorphic insects the cuticle of the pupa is formed beneath the larval cuticle, and later the cuticle of the imago beneath the pupal. As to the main regions of the body, it is found that in cases where these regions are typically represented in the larva, the cuticle of each is formed ready for pupation, from discs derived from the skin of the corresponding part of the larva. These discs may however grow so as to lie beneath other regions of the larval cuticle. For example, in the grub of the midge Chironomus[1] the brain is situated in the first thoracic segment, and the imaginal discs of the head, including those of the eyes and feelers, grow backwards towards the brain. In the maggots of blue-bottles[2] and their allies, the mouth, opening at the narrow front extremity of the body, leads into a spacious chitin-lined cavity usually styled the pharynx (Fig. 86 A H), but probably to be regarded as the inpushed larval head.

[1] L. C. Miall and A. R. Hammond: "The Structure and Life-history of the Harlequin Fly (Chironomus)". Oxford, 1900.

[2] J. Van Rees: "Beiträge zur Kenntniss der inneren Metamorphose der Musca vomitoria". *Zool. Jahrb.* (*Anat.*), III. 1888.

In paired pouches of this cavity, reaching back to the brain, which lies in the hind thoracic region of the larva, are found the imaginal discs for the eyes (Fig. 86 A *e*) and feelers (Fig. 86 *f*), which appear on the surface during the pupal stage when the aforementioned pouches become everted (Fig. 86 B C).

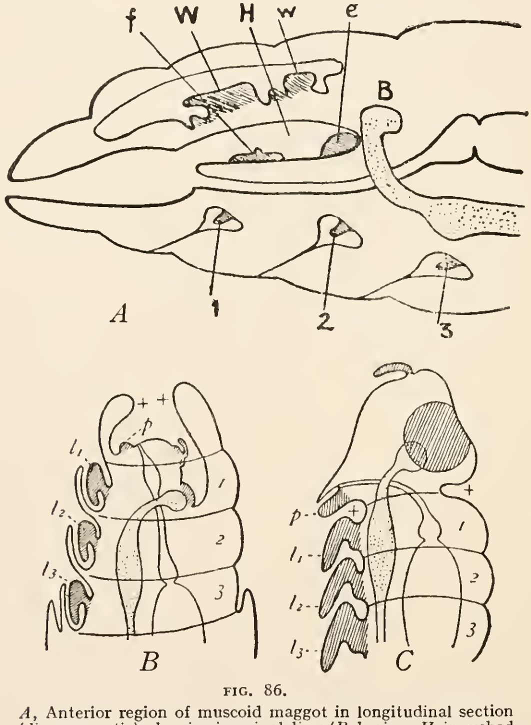



FIG. 86.

*A*, Anterior region of muscoid maggot in longitudinal section (diagrammatic), showing imaginal discs (*B*, brain; *H*, inpushed head region; *e*, eye; *f*, feeler; *W*, forewing; *w*, hind-wing; 1, 2, 3, legs). *B*, The same in last stage, with legs ($l_1$, $l_2$, $l_3$) incipiently jointed and partly outpushed (*p*, disc of proboscis). *C*, Formation of pupa by outpushing of head-capsule with appendages and legs. *A*, from Carpenter, "Life Story of Insects"; *B*, *C*, from Comstock, "Introduction to Entomology." After Kowalevsky, Van Rees, and Lowne.

The legs of pupa and imago are formed from buds or discs growing in pouches directed inwardly from the body-wall of the thoracic segments of the larva (Fig. 86 A, 1, 2, 3). These leg-buds increase in complexity as their segmentation becomes apparent through a partial division of the originally simple bud and the lengthening of regions at first telescoped into one

another (Fig. 86 B C). In those larvae which possess thoracic legs—such as the grubs of many beetles or the caterpillars of moths—the outpushed legs of the pupa may lie partly within the corresponding larval legs during the final larval stage. It was long ago noticed that if one leg of a fully-grown caterpillar were cut off the resulting butterfly emerged with a mutilated foot, the terminal portion of the relatively long, segmented leg of the pupa projecting into the short limb of the final larval instar. In larvae that differ most profoundly

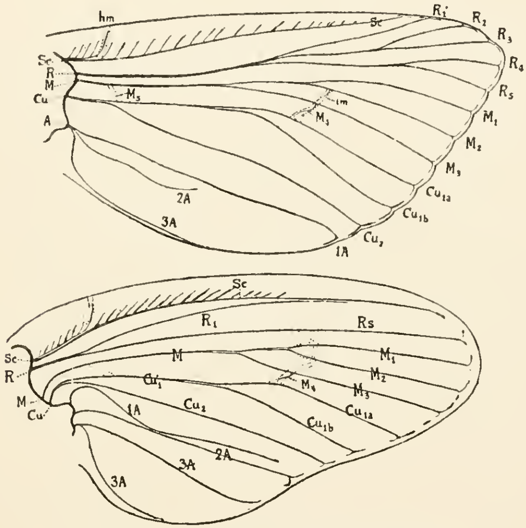



FIG. 87. PUPAL WINGS OF MOTH (*Xyleutes*).
Showing tracheal tubes prefiguring nervures. Lettering as in Fig. 35. × 2. After Tillyard, *Proc. Linn. Soc. N.S. Wales*, XLIV.

from the perfect insect, such as the maggots of house-flies and blue-bottles, the imaginal leg-buds (Fig. 86 A) grow far into the interior of the body, each retaining its connexion with the outer body-wall only by a slender stalk or chain of cells.

Finally we pass to the origin of the wings themselves.[1] It has been already mentioned (ch. ii, pp. 63–4, Fig. 34) that a wing-bud appears as a small pad growing into a pouch

[1] J. Gonin: "Récherches sur la Métamorphose des Lepidoptères". *Bull. Soc. Vaud. Sci. Nat.* XXXI. 1894. W. F. Mercer: "The Development of the wings in Lepidoptera". *Journ. New York. Entom. Soc.*, VIII. 1900.

inpushed from the larval body-wall. The bud first arises as a thickening of the epidermis, due to increasing depth of certain cells ; these thickened cells form an enlarging region which becomes folded on itself and enclosed in the pouch due to the ingrowth of a sheet of thin cells from the skin. In close association with the growing wing-bud is a tracheal trunk, from which air-tubes grow into the space between the bud's two folds. The arrangement of these tubes foreshadows the plan of nervuration in the developed wing, for the sub-costal, radial, cubital and anal systems of longitudinal nervures or at least some of them are represented by the growing air-tubes (Fig. 87). It is remarkable that while a lacewing, a butterfly or a moth-pupa has a wing with the full set of tracheal trunks, in the pupal wing of a scorpion-fly or a caddis-fly only two or

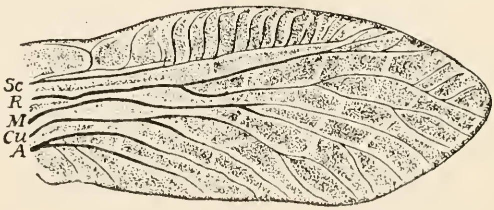



FIG. 88. WING OF PUPAL ALDER-FLY (*Sialis*).
Showing tracheal tubes and pale bands which indicate course of nervures (*Sc*, subcostal ; *R*, radial ; *M*, median ; *Cu*, cubital ; *A*, anal). $\times 5$. After Comstock, " Wings of Insects ".

three trunks are apparent. As during the final larval stages, the pupal body begins to take shape and the wing-buds are thrust out from their pouches, narrow pale bands (Fig. 88) can be distinguished forming tracks as it were in which the air-tubes lie ; these tracks show where the thickenings of the wing-cuticle that form the completed nervures are becoming defined.[1] Within these thickenings which assume a more or less cylindrical form around long blood-spaces, the air-tubes become enclosed, while over the rest of the area of the developing wing the upper and lower surfaces become approximated, so that when the cuticle has dried and hardened an apparently simple and firm membrane is provided for the purpose of flight.

[1] J. H. Comstock : " The Wings of Insects ". Ithaca, New York, 1918. R. J. Tillyard : " The Panorpoid Complex ". Pt. III, " The Wing-Venation", *Proc. Linn. Soc., N.S.W.*, XLIV. (pt. III), 1919.

CHAPTER V

# SOME WINGLESS INSECTS

IN an earlier chapter of this book reference has been made to insects, such as most of the aphids or " greenfly ", in which winged and wingless forms may occur, seasonally or otherwise, in the life-history of the same species ; as well as to others, such as scale-insects and certain cockroaches, in which the male is winged while the female is wingless, a condition found also in not a few insects which undergo the hidden type of wing-growth, such as the common glow-worm among the beetles, and the notorious "Winter" and " Vapourer" moths. More rarely the male and not the female is the sex destitute of wings. It is of interest to find that among those highly-organized social insects, the ants, the vast majority of members of the enormous families that grow into communities, are " workers "—strangely modified, infertile females, all of them wingless ; while among the termites—so called " white ants "—the wingless workers and soldiers may be modified infertile individuals of either sex. In many families of insects whose members are normally winged, species wingless in both sexes may be found ; earwigs and psocids or " book-lice " afford examples of this condition. Reference will be made to such in the present chapter, but it is proposed to direct attention especially to certain orders or large groups of insects all of whose members are destitute of wings.

This wingless condition is frequently the accompaniment of a parasitic mode of life, and a typical example of such wingless parasites is afforded by the lice (Anoplura)—an order, possibly allied to the bugs (Hemiptera). Lice (Fig. 89 *a*) have prominent heads with short feelers, and a remarkable suctorial mouth provided with recurved hooks (*b*), which serve to fix to the host-animal on which the parasite lives and to pierce its skin, and a delicate protrusible tube through which

blood can be sucked in. The legs are short and robust, the shin being immensely broadened towards its tip which is produced into a blunt outgrowth bearing strong spines (Fig. 89 *f*). Just at the base of this is a ridge or pad beset with spines—short, fine and sharp. The foot-region consists of one very short segment which bears a single strong curved claw so arranged that in conjunction with the pad and spines of the shin, it clasps a hair of the host-animal. These structural details have been mentioned to emphasize the fact that lice are parasitic insects, which, while degraded on account of the absence of wings, are very specially adapted for clinging

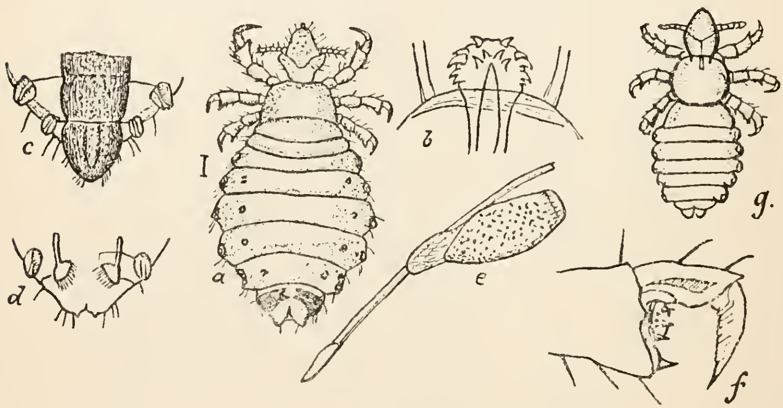



FIG. 89. CATTLE-LOUSE (*Haematopinus eurysternus*).
*a*, female. × 15. *b*, rostrum with hooks. × 120. *c*, ventral view of male's abdominal extremity; *d*, of female's. × 30. *e*, egg attached to hair. × 15. *f*, tip of shin with foot, claw and pad. × 120. *g*, young. × 30. *a*—*e*, from Osborn, *U.S. Dept. Agric. Ent. Bull.* 5.

to the hairs of large animals and sucking their blood. The adult male louse has an extensive, strongly chitinized plate or tube below the abdomen (Fig. 89 *c*) protecting the genital armature, while the female has, at the tip of her abdomen, a pair of strong claspers (Fig. 89 *d*), which hold the eggs. A louse's egg-case (Fig. 89 *e*) is a distinctly graceful, sculptured object attached after laying, by means of secreted cement, to a hair of the host-animal. From this egg is hatched a young insect (*g*) which in the general form of its body, its highly specialized suctorial mouth and clinging feet is a nearly exact miniature of its parent. Only the distinctively sexual structures concerned with reproduction are wanting, and

these are not seen in the immature louse during the four or five stages through which it grows into the adult condition. But if a louse late in the last stage but one be examined, these characteristic structures of the adult can be detected in the cuticle which—beneath that in present use—is being prepared for the final moult. The wingless lice give us, therefore, an example of an insect life-history in which growth is accompanied by the least degree of change—a life-history without transformation. And we realize that this condition is appropriate to creatures which pass their whole existence, from the egg to the adult stage, in the curiously specialized and uniform surroundings afforded by the bodies of their hosts.

Besides these blood-sucking lice (Anoplura), specimens of another order of parasitic wingless insects are to be found clinging to the hairs of mammals ; these are " biting-lice " (Mallophaga, Fig. 90), though the great majority of them live on the bodies of birds. They are superficially rather like the Anoplura, but may be readily distinguished by their entirely different mouth-parts ; for a mallophagan possesses, instead of a suctorial tube, strong paired mandibles, rather like those of a grasshopper, and the insects feed by biting or nibbling at the feathers or hairs and skin of their hosts. In one of the families the foot bears the two claws usual among insects and these Mallophaga (which live on birds) may be able, if their host die, to go in search of a fresh one. Here then is an example of periods of parasitism alternating with intervals of migration. But many biting-lice have a single-clawed foot (Fig. 90 *a*) adapted for clinging, essentially similar to that of a blood-sucking louse, and Mallophaga of this type spend the whole of their lives—from the egg to the adult state—attached to hair or feathers on the bodies of their hosts, and as the newly-hatched young resemble closely their parents in all essential features and in most points of structural detail, they also afford an example of a group of parasitic insects, wingless throughout life whose growth is unaccompanied by any marked degree of change.

These Mallophaga or biting-lice are now generally regarded as a distinct order of insects, but few students doubt that they show affinity to the Corrodentia (the book-lice and their allies) and some classifiers of insects still prefer to regard the

Mallophaga as a sub-order of the latter. Among the *Psocidae*, the family which represents the Corrodentia in these countries, are found many small insects with relatively ample wings that live on the bark of trees, in moss, and other vegetable growth. It is of interest to find that in several genera of these psocids —*Mesopsocus* for example[1]—the wings in many adults remain in the condition of short pads or rudiments, like those of young, growing insects ; within the same species wings may or not be be developed. The best known of the *Psocidae* is probably

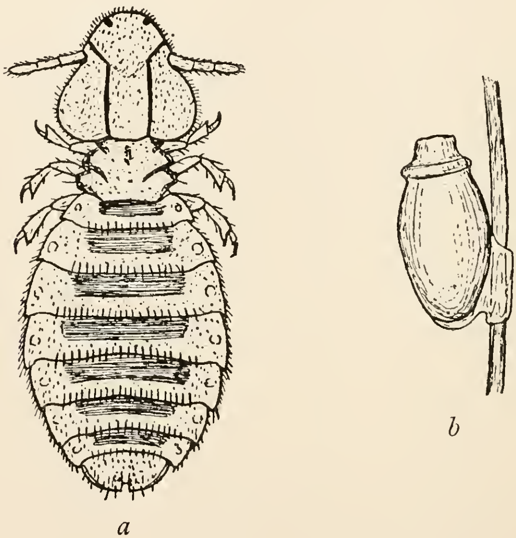


FIG. 90. CATTLE-BITING LOUSE (*Trichodectes scalaris*). *a*, female ; *b*, egg. × 24. From Carpenter, *Econ. Proc. R. Dublin Soc.* II.

the tiny pallid insect *Atropos divinatoria* which may be seen running about in decaying dry wood, among old books and papers or in neglected natural history collections ; this creature is often known as a " death-watch " because of the tapping noise—audible in the silence of night—which it makes with its mandibles on wood or other material in which it lives. Now Atropos has no trace of wings in any stage of its life-history, resembling in this respect the whole of the Mallophaga.

[1] P. Bertkau : " Ueber einen auffallenden Geschlectsdimorphismus bei Psociden ". *Arch. f. Naturgesch.*, XLIX., I. 1882.

Another tiny whitish psocid (*Clothilla pulsatoria*) rarer than Atropos but similar in its mode of life, has minute wing-rudiments in the adult state ; as in the forms of Mesopsocus mentioned above, the wingless condition has not been fully attained, or, as the process is often described, wings have not been altogether lost. The varying condition as regards wing-development in members of the same family and the same species suggest inevitably that this mode of expression is justified, and that in such a group of the Mallophaga, whose relationship to the winged *Psocidae* is admitted, we may conclude that the normal growth of wings has been entirely suppressed as an accompaniment of their parasitic mode of life. It is worthy of mention that, while among the winged psocids, the prothorax is extremely reduced in extent so as not to be visible from above, it retains its original importance in the plan of the body in those members of the family whose wings are reduced or wanting. Such a fact points to the wingless condition as of the nature of a reversion to primitive or immature conditions.

Some modern students[1] of the Anoplura—the true or sucking lice—consider them to be allied to the Mallophaga despite the suctorial nature of the anopluran mouth, which has been generally held to indicate affinity to the Hemiptera—the order which comprises bugs and their allies. In connexion with the subject of winglessness as an accompaniment of parasitism, it is instructive to turn to a notorious member of the Hemiptera, the Bed-bug (*Cimex lectularius*, Fig. 91). This hairy, hard-cuticled little parasite, with its prominent eyes and lobed prothorax, its broad, rounded abdomen, and its flattened form adapted for concealment in cracks and crevices, has the hindwings entirely wanting, while the forewings are represented by small, firm, hairy pads. Besides the development of these pads, the only noteworthy change experienced during the bed-bug's life-history is the elaboration in form of the prothorax, which, undistinguished in the newly-hatched young, has in the adult two prominent, forwardly-directed, rounded lobes. It is interesting to find that the family (*Cimicidae*) to which the bed-bug belongs comprises

[1] E. Mjöberg : " Studien uber Mallophagen und Anopluren ". *Ark. f. Zool. (Stockholm)*, VI. 1901.

genera, such as *Ceratocombus*, in which the forewings, though relatively long are imperfectly developed, and others, *Microphysa* for example, in which these organs are normal in the male but abbreviated or rudimentary in the female. It is suggestive to recognize a tendency towards the wingless

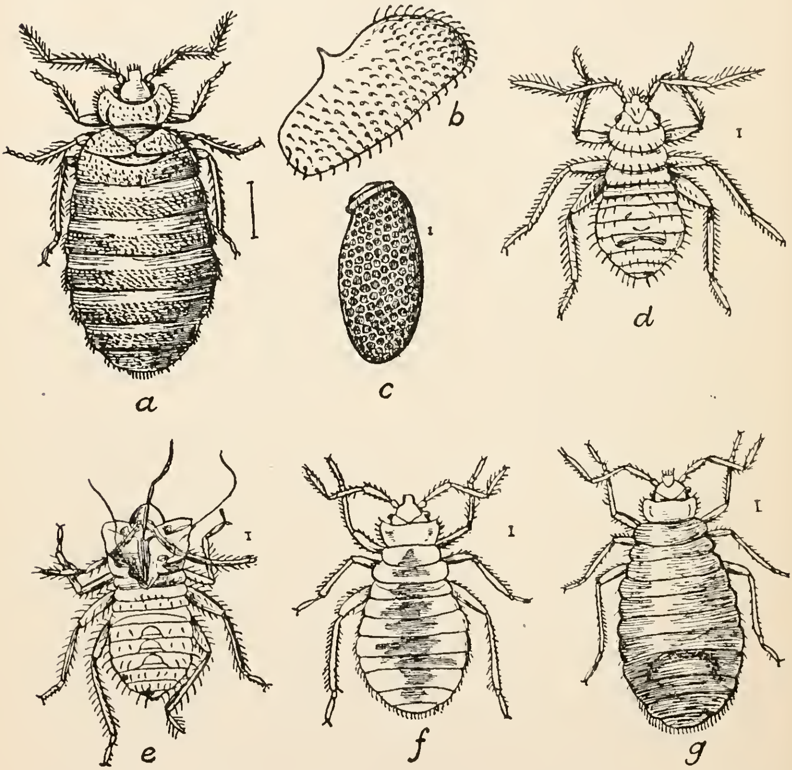



FIG. 91.

*a*, Bed-bug (*Cimex lectularius*), female. ×5. *b*, vestigial wing. ×20. *c*, egg; *d*, young in first stage; *e*, cast cuticle of first instar; *f*, second instar just after moult; *g*, second instar after feeding. × 25. After Marlatt, *U.S. Dept. Agric. Entom. Bull.* 4.

condition, in the allies of those insects wherein complete winglessness accompanies the parasitic mode of life.

In the opening pages of this chapter reference was made to the occurrence of wingless insects among the orders which undergo the hidden process of wing-growth and pass through a marked transformation in the course of their life-history.

Such cases, though relatively few, are not rare among beetles, moths and two-winged flies, and the well-known parasitic group of the Fleas[1] afford an example of an entire order (the

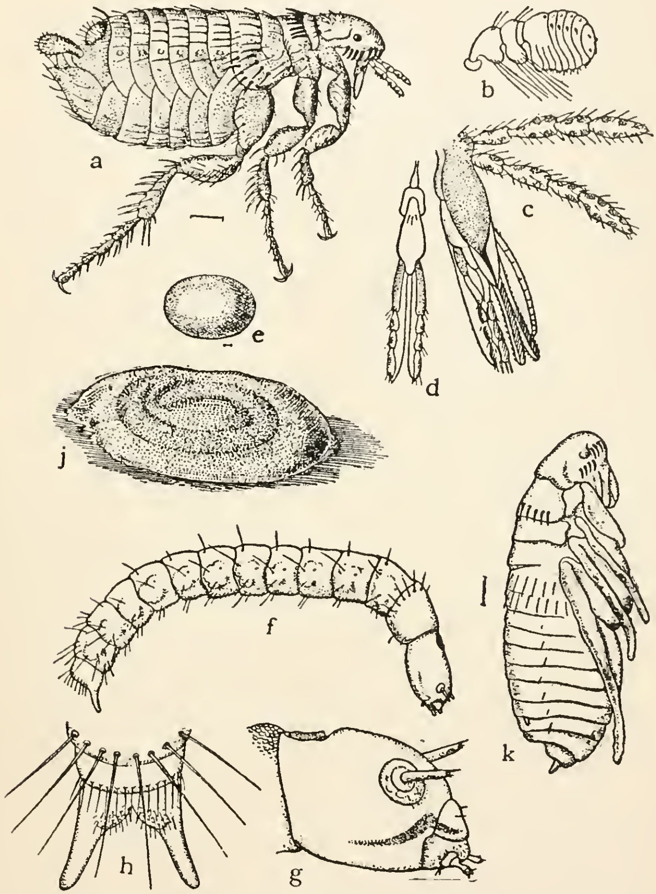



FIG. 92.

*a*, Dog-flea (*Ctenocephalus canis*), male (side view). ×12. *b*, feeler. × 200. *c*, jaws; *d*, labium. × 50. *e*, egg; *f*, larva, (side view), ×12. *g*, head of larva; *h*, tail-region. ×300. *j*, cocoon; *k*, pupa. ×12. From Howard, *U.S. Dept. Agric.*

Aphaniptera) of metamorphic insects with wings absent or reduced to the merest vestiges. The general aspect of an ordinary flea (Fig. 92 *a*) with its body strongly compressed from side

[1] H. Russell: "The Flea". Cambridge, 1913. F. C. Bishopp: "Fleas". *U.S. Dept. Agri. Bull.* 248. 1915.

to side, its small rounded head and its elongate spiny legs is highly characteristic. Eyes, as in the Anoplura and Mallophaga, are absent entirely, or much reduced. The short, stout feelers (Fig. 92 *b*) are sunk in pits on either sides of the head; the feeler has two relatively broad basal segments, succeeded by possibly ten, short and still broader segments, crowded together and imperfectly distinguished from each other, forming a terminal club. The upper lip (*labrum*) and the mandibles are elongate piercers with saw-teeth on their edges, forming in combination a suctorial tube and lying between and in front of the short flattened maxillae, each with its four-segmented palp; these palps project conspicuously downwards and forwards from the head, looking like feelers (Fig. 92 *c*). The labium (*d*) is prolonged into a "beak" and bears a pair of thickish palps which serve as sheaths for the piercing organs of the mouth. Thus the flea is admirably provided for its occupation of blood-sucking. The thoracic segments often bear rows of spines ("combs") and sometimes small scale-like plates, which have been regarded, though doubtfully, as vestigial wings. The spiny legs are remarkable for the relatively enormous size of their haunches (*coxae*) and their strong claws; fleas are thus adapted for leaping from one host to another and for clinging to the host's hairs or feathers.

Fleas' eggs (Fig. 92 *e*) are oval in shape, with smooth, white cases, which often resemble birds' egg-shells in miniature. They are not, like the eggs of lice, fastened to the host's hairs, but fall into crevices of its nest or dwelling-place. From these eggs are hatched after a few days eruciform larvae (Fig. 92 *f*) with distinct head and fourteen body-segments, which are destitute of legs, but bear tubercles with long bristles, while outgrowths possibly suitable for adhesion, are present at the tail-end. The newly-hatched flea-grub may possess a spine on the head which serves to break the egg-shell; this structure is not present in the later larval stages, of which there are two or three. The flea-grub's head (Fig. 92 *g*) bears short feelers and biting mandibles, by means of which it feeds on organic particles in the nest or other matter among which it lives. The larva of *Pulex irritans*, the flea which commonly infests mankind, lives in the crevices between the boards of floors

and wooden beds, while grubs of cat and dog fleas may be found among the bedding material provided for those domestic pets. It has been stated that in many cases the grub must have as part of its food "half-digested blood passed through the parent flea's body".[1] The length of the larval period varies in different kinds of fleas, and under different conditions of climate, from less than a week to four months.

When fully grown, the flea-grub spins a cocoon (Fig. 92 *j*) by fastening together, with silky secretion, fragments of its dwelling place; such a cocoon is round or oval in shape, and naturally inconspicuous on account of its composition. Within this cocoon the last larval cuticle is cast and the pupa (Fig. 92 *k*) revealed; the pupal stage, even in the same species, may vary in duration from less than a week to more than a year. In the pupa the characteristic features of the adult are clearly recognizable, having been formed, as in metamorphic insects generally, from imaginal buds. The life-history of a flea affords, therefore, the interesting condition that it resembles closely that of an insect which undergoes the hidden type of wing-growth, although no wings are ever developed.

The larvae of fleas resemble in general aspect those of certain midges and other insects belonging to the order of the two-winged flies (Diptera) with which the fleas may have some affinity. In any case it is of interest to trace how, among certain members of the Diptera the parasitic habit is accompanied by a reduction in size or total disappearance of the wings. Many Diptera of various families—such as breeze-flies, gnats, the stable-fly (*Stomoxys*) and the African Tsetse (*Glossina*) habitually suck blood from large animals; these all fly actively, resting perhaps, for a short time on the body of the victim and then darting away again. But the Forest-fly (*Hippobosca*), which often attacks horses in the south of England, is provided with strong clinging claws as well as with adhesive pads and plumose hairs, which enable it to hold on to the hairs of the animal whose blood it draws. It happens, therefore, that these insects often spend a long time on the bodies of their hosts, scores or more than a hundred of them being sometimes found crawling over the body of a single

[1] J. Waterston: "Fleas as a Menace to Man and Domestic Animals". *Brit. Mus.* (*Nat. Hist.*) *Econ. Series No.* 3. London, 1916.

animal.[1] The wings of Hippobosca, though of a normal length are narrow and feeble in texture for an insect of such bulk. Allied flies (*Lipoptera*) that attack deer, are observed usually to cast or tear off their wings after resting on the skins of the beasts on which they feed; here, therefore, we notice an artificial loss of wings in the life-time of each insect. Other members of the same family that infest the nests of birds and feed on their blood (such as *Stenopteryx*) have the wings so abbreviated or so narrow as to be useless for

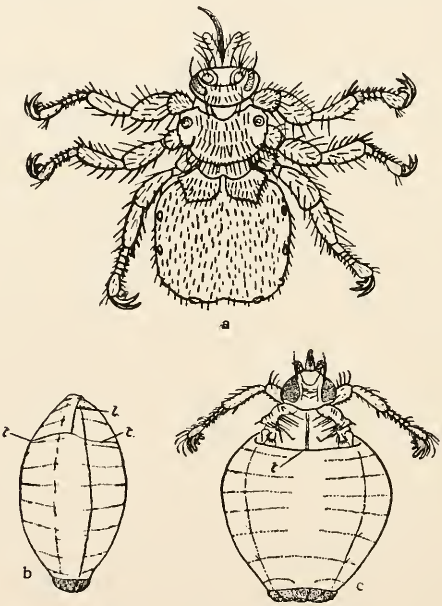



FIG. 93.
*a*, Sheep-ked (*Melophagus ovinus*). ×8. *b*, Puparium of *Ornithomyia* (side view) (*t*, transverse suture; *l*, lateral suture); *c*, the same, dorsal view with fly emerging. ×8.

flight. It is not surprising to find that some allied genera are entirely wingless, for example the keds (*Melophagus*, Fig. 93 *a*) which frequently infest sheep, being found in numbers clinging to their wool.

These curious parasitic Diptera, which show in their various groups the degeneration or the total disappearance of wings, have all a very remarkable life-history. The egg is hatched

[1] E. A. Ormerod: "Report of Observations of Injurious Insects". London, 1895, 1898.

within the mother's body and the larva, nourished by a milky maternal secretion, is not born until it has attained its full growth. Quickly after birth, the larval cuticle becomes converted into a puparium (Fig. 93 *b c*) within which the pupa is formed, and from which, later on, the perfect insect emerges, the development being thus a curious and extreme modification of the type found in the blue-bottle group.

In the maggot of Melophagus for example, may be detected[1] the inpushing that gives rise to the adult head-capsule, and imaginal buds of the feelers, jaws and legs corresponding closely to the similar structures in the larva of a house-fly or blow-fly. This life-history would in itself stamp the wingless

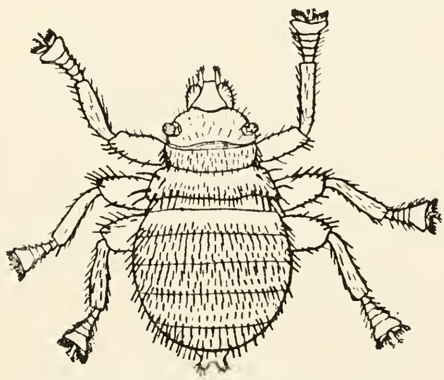


FIG. 94. BEE "LOUSE" (*Braula caeca*). × 24.
From Carpenter, *Econ. Proc. R. Dublin Soc.* II.

insects that undergo it as degraded muscoid Diptera, and there are two other families of wingless parasites—the strange *Nycteribidae* of bats and the minute *Braulidae* (Fig. 94) that live on bees—not closely related to the Sheep-ked, the former at least showing by their similar development that they belong to the same great section of the two-winged flies, though no trace of wings is apparent on them at any stage.

A mode of development, in some respects parallel to that displayed by the *Hippoboscidae* and their allies, but carried farther, is shown in those most remarkably aberrant Diptera,

[1] H. S. Pratt: "Beiträge zur Kenntnis der Pupiparen. Die Larve von Melophagus ovinus". *Arch. f. Naturgesch.*, LIX. 1. 1893.

the *Termitoxeniidae*[1] which live as "guests" in the nests of some species of termites ("white ants") inhabiting Africa and Southern Asia (Fig. 95). Wings are recognizable as small strap-like vestiges on the mesothorax; these probably serve to attach the curious insects to their termite-hosts. The abdomen, with its thin white cuticle has the hinder-end directed forwards beneath the thorax, and becomes distended with the food which is sucked from the bodies of the termites pierced by the suctorial mouth-organs of the Termitoxeniae which behave as parasites in the habitations that shelter them. The development of these creatures is absolutely exceptional among

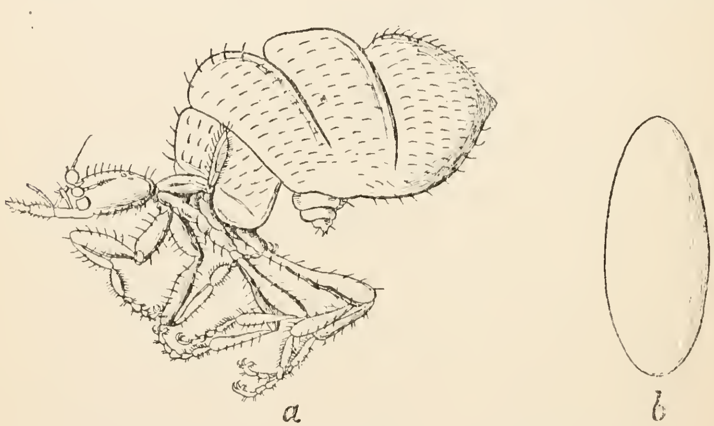


FIG. 95.

*a*, *Termitoxenia Heimi*, female from nest of *Termes obesus*, S. Africa (side view). × 25.
*b*, egg of *Termitoxenia Havilandi*, from nest of *Termes latericius*, S. Africa. × 35.
After Wasmann, *Zeitsch. f. wissensch. Zool.* LXVII.

insects. They are hermaphrodite, the testes developing first —the ovaries, each consisting only of a single ovarian tube later. The egg (*b*) is of relatively enormous size, and in the genus *Termitoxenia* gives rise after hatching to an adult, which except for its slender abdomen resembles the parent. In *Termitomyia* the egg is hatched within the parent's body and the young insect is born in the adult condition. Thus, the typical transformation is altogether wanting. From the structure of the feelers, the *Termitoxeniidae* belong to the muscoid

[1] E. Wasmann: "Termitoxenia ein neues flügelloses physogastres Dipterengenus aus Termitennestern". *Zeitsch. f. wissensch. Zool.*, LXVII. 1901.

section of the Diptera—that section in which, as we have seen, the transformation is, as compared with that of all other insects, the most profound. It is the more remarkable, therefore, to see how along with a highly specialized form of parasitic life, there has come about, not only a loss of wings, but the total disappearance of metamorphosis, and even of the succession of moults almost universal in the life-history of all Arthropoda.

These and many similar facts supply ample justification for the oft-used expression that such wingless, parasitic insects as we have been considering, have " lost their wings ", and the same result is seen to accompany other abnormal life-conditions. Such absence of wings is a secondary, not a primitive character. It is instructive in this connexion to refer to some famous recent researches on the facts of heredity[1] as shown by small two-winged flies (*Drosophila*) whose larvae feed in fruit. In the course of long series of generations of these quickly-breeding insects, kept under careful observation, it has been found that reduction or abortion of the wings may occur in certain individuals and that these suddenly-arising modifications are inherited according to definite rules. It is noteworthy that the extreme condition of degeneration when the wings are reduced to the merest vestiges, is not reached through a long series of ancestors showing gradual retrogressive change, but may appear suddenly, as what is termed a *mutation*, in the offspring of fully-winged parents. There is no doubt that such changes are due to changes in that substance of the nuclei of the reproductive cells—the germ-plasm, as it is called—which contains the factors or determiners of inborn characters. The cause of such changes in the germ-plasm remains, however, for the present beyond the bounds of our knowledge.

But, besides such wingless insects as those we have considered, there are others, briefly referred to in the introductory chapter (p. 3), which have no apparent near relationship to winged groups. These—the spring-tails and bristle-tails, with their more obscure allies—are believed to be primarily wingless, not only because they have no close affinity with

[1] T. H. Morgan and C. B. Bridges : " Sex-linked Inheritance in Drosophala ". *Carnegie Publication No.* 237. Washington, 1916.

any winged forms, but also because they exhibit a combination of primitive characters which marks them out as probably representing offshoots of the ancestral stock of the whole class of insects as they might be imagined to have existed before

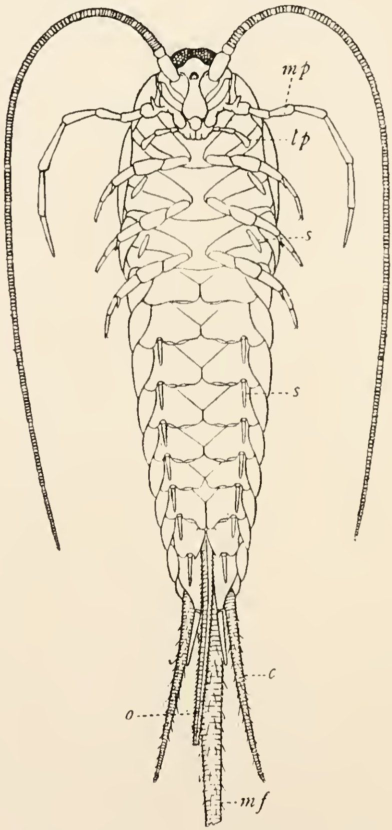



FIG. 96. ROCK-JUMPER (*Petrobius*), FEMALE, VENTRAL VIEW. *mp*, maxillary palp; *lp*, labial palp; *s*, stylets; *o*, ovipositor; *c*, cercus; *mf*, median tail-process (truncated). × 3. From Comstock, "Introduction to Entomology".

the development of wings. This small, but highly interesting assemblage of orders is known therefore as the Apterygota, and is sharply distinguished in classificatory systems from the winged groups.

As a typical example of the Apterygota we may take a specie

of " rock-jumper " one of the bristle-tails (or Thysanura) some species of which may be found in abundance along the sea-shore just above high-water mark, and others among stones or vegetation in inland localities. The insect (Fig. 96) has the head and body covered with beautiful scales which give it a dark

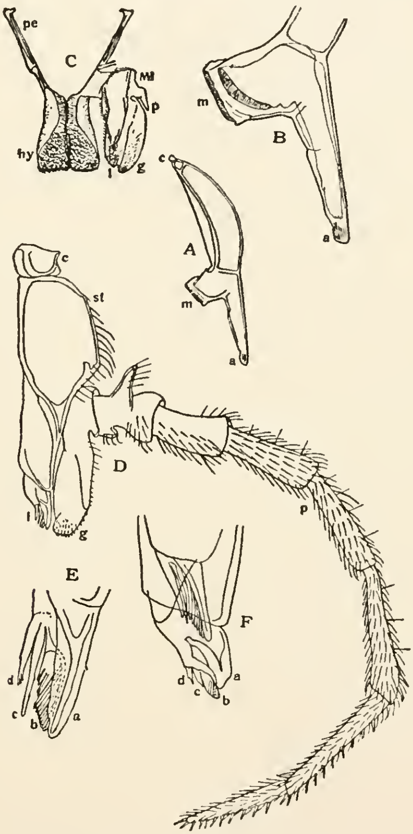



FIG. 97. JAWS OF ROCK-JUMPER (*Petrobius brevistylis*). A, mandible (*c*, condyle; *a*, apex; *m*, molar area). ×13. B, terminal region of mandible (penultimate instar); the new cuticle can be seen within. ×36. C, Hypopharynx (*hy*) front aspect, with the left maxillula (*Ml*) slightly displaced laterally, but retaining its membranous connexion with the base of the hypopharynx (*l*, lacinia; *g*, galea; *p*, palp of maxillula; *pe*, peduncle of hypopharynx). D, Maxilla, hinder aspect (*c*, cardo; *st*, stipes; *l*, lacinia; *g*, galea; *p*, palp). × 18. E, Head of lacinia showing apex (*a*), " brush " (*b*), and acute processes (*c* and *d*). F, Head of lacinia from a specimen in the penultimate stage, showing apex (*a*), " brush " (*b*), and acute processes (*c* and *d*) greatly worn, and new cuticle of head formed within. × 60. After Carpenter, *Irish Nat.* XXII.

lustrous appearance as it runs and jumps rapidly and with agility among the stones and rocks of the tidal margin. The feelers on the head are long and many-jointed. Examining the jaws we find that the mandibles (Fig. 97 A) differ from those of any adult winged insect and resemble those of certain Crustacea, having an elongate, tapering basal region, a central ridged grinding area and a toothed apex, while the maxillulae (Fig. 97 C)—those minute appendages between the mandibles and maxillae—are quite well developed and hinged on to the base of the tongue. Attached to the haunch of each thoracic leg is a short unjointed stylet (Fig. 96 *s*), and similar structures are found in pairs on each abdominal segment from the second to the ninth inclusive, the hinder ones being relatively long. The abdominal segments also carry curious little bladder-like "exsertile vesicles", and on the eighth and ninth segments are paired "genital processes", those of the female forming the ovipositor (Fig. 96 *o*). The tenth abdominal segment bears a pair of elongate many-jointed cerci (*c*), and a median tail-filament (*mf*), of similar aspect to these, projects between them from the tip of the abdomen. It will be realized that such an insect differs from a grasshopper or beetle, not only on account of the absence of wings, but by the possession of crustacean mandibles, prominent maxillulae, and a series of paired limbs on most of the abdominal segments.

Some recent studies[1] of the life-history of such insects, show that there are at least five stages before the adult condition is reached, and that in the first two of these the young insect is devoid of scaly covering, has no stylets on the haunches of the legs and no trace of genital processes. In the third stage scales are present and the haunch-stylets are recognizable, though small, but the genital processes are still wanting. These appear in the fourth period of the life-history, but they are short, and, in the female, do not show the ringed aspect which characterizes them in the developed ovipositor. It is of great interest to be able to trace changes, that if not very profound are markedly recognizable in the life-history of these primitive wingless insects. In a specimen late in

[1] R. Heymons: "Ueber die ersten Jügendformen von Machilis". *Sitzgs. Gesellsch. naturforsch. Freunde, Berlin.* 1906. K. W. Verhoeff: "Ueber Felsenspringen, Machiloidea. Die schuppenlosen Entwicklungstufen". *Zool. Anz.*, XXXVIII. 1911.

the last stage but one, the new cuticle of mandible and of the beautiful and delicate extremities of the adult's maxilla can be clearly seen (Fig. 97 *B*, *F*) beneath the old cuticle now worn down by use.

The other considerable order of the Apterygota are the Collembola or spring-tails. These (Fig. 98) are curiously modified insects, with short feelers (usually four segments only), no compound eyes but a group of (usually eight) ocelli on each side of the head, the mouth region inpushed so that the jaws appear to be retracted into the head, only six abdominal

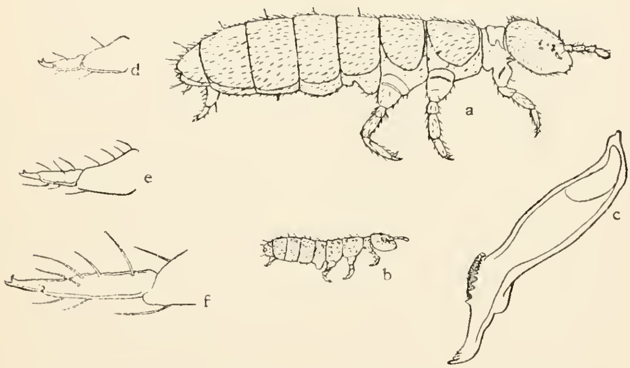



FIG. 98. SPRING-TAIL (*Cryptopygus crassus*), GRAHAMLAND, ANTARCTICA. *a*, adult (side view); *b*, young specimen. ×25. *c*, mandible; *d*, *e*, *f*,, three stages in growth of spring. ×160. After Carpenter, *Proc. R. Soc. Edinb.* XXVI).

segments, the first of which has its appendages modified into an adhesive ventral tube, while the limbs of the third and fourth are respectively specialized as a minute pincer-like toothed "catch" (Fig. 99 *a*), and a more or less elongate "spring", which consists of a basal median piece (*manubrium*) to which are jointed a pair of processes (*dentes*) usually flexible, each terminating in a toothed claw (*mucro*). This spring can be held directed forwards beneath the body by the catch which grips the manubrium between the two dentes. When the catch releases the manubrium, and the extensor muscles of the spring contract, the spring is pulled strongly downwards and backwards so as to strike the ground and the insect jumps into the air for a distance that may be described as enormous, as compared with its own size.

A young spring-tail newly-hatched, differs from its parent in no important respect. Among the modifications common within the order, a reduction of the spring is strongly characteristic in certain genera, and this may be carried so far that the organ becomes a mere vestige or vanishes entirely. This retrogressive change in the spring can be traced in some spring-tails in the course of the life-history. For example, in a Triacanthella, the adult shows no junction between dens and mucro, but the newly-hatched young may possess a spring in which these parts are clearly recognizable (Fig. 99) recalling the condition found in allied genera—such as *Achorutes*—which have the various elements of the spring developed normally, though remaining relatively small.

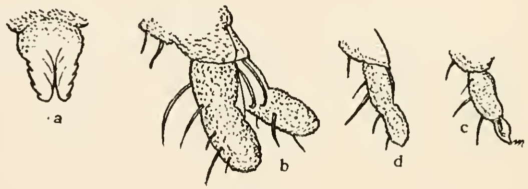



FIG. 99. ABDOMINAL APPENDAGES OF SPRING-TAIL (*Triacanthella alba*), CAMPBELL ISLAND.

*a*, "catch"; *b*, spring of adult viewed obliquely (paired dentes without mucrones); *c*, *d*, spring (side view) of very young; (*c*) and half-grown (*d*) specimens; in the former is a distinct mucro (*m*) which disappears in later stages. × 280. After Carpenter, "Sub-antarctic Islands of New Zealand", XVII.

Summing up the facts briefly reviewed in this and previous chapters, we see that secondary winglessness is a condition that has appeared again and again in various orders of insects, in some cases associated with parasitism or some abnormal mode of life, in others rather with an abundant food-supply available without the necessity for migration—as with the wingless generations of virgin aphids, and possibly in the experimental series of Drosophila. The wingless condition of the adult may be correlated with a normal type of life-history, either exopterygote, as in the case of the aphids and the lice, or endopterygote, as in the case of the fleas. On the other hand such wingless parasites as Melophagus, exhibit a most unusual type of life-history, though one which can be seen also among their winged relations, while in Termitoxenia

winglessness is accompanied with a total suppression of the preparatory stages.

Insects which may be regarded with any degree of probability as primarily wingless, are relatively very few when compared with the whole class. It is of importance to notice that in those which may be regarded as distinctly primitive (the *Machilidae*) there is a definite, though inconspicuous, process of change in the course of growth. From this fact we gain perhaps a suggestion as to the existence of some such process in the life-histories of the ancient, ancestral insects, from which the startling transformations of their modern descendants may be regarded as having been elaborated.

## CHAPTER VI

# THE CLASS AND ORDERS OF INSECTS

IN the course of the preceding chapters, it has been necessary to make occasional reference to orders and other classificatory groups in which the insects, whose life-histories have been sketched, are arranged by systematic naturalists. With the leading facts of insect structure and growth thus reviewed, it seems now advisable to set forth a condensed summary of these classificatory groups, so that before passing on to other aspects of the subject, we may take a general survey of the whole class of insects and realize the varying degrees of likeness and difference that are to be found among them. And in this survey, as is appropriate to the subject of the book, especial attention will be paid to the life-histories.

Early in Chapter II (p. 5–6), the Insects were defined as a Class of the great group or Phylum of the Arthropoda, the leading structural characters of which were subsequently pointed out. The jointed cuticle or exoskeleton, which forms the most obvious outward feature of these animals, involves, as was seen, the necessity for a series of moults throughout the life-history, and here we see one of the foundation-facts connected with insect transformation. In the great sub-kingdom of the Arthropoda are included, together with Insects, several other large classes of animals which display the same general type of structure. For example, there are the CRUSTACEA (water-fleas, barnacles, shrimps, lobsters, crabs) in most of which two pairs of feelers are present, and limbs are borne on most of the segments of the body, many of these limbs being two-branched (biramous) and some of them usually having gills, adapted for breathing dissolved air, closely connected with them. There are the CHILOPODA (centipedes), elongate, flattened creatures which resemble insects in having only one

pair of feelers and in breathing by means of air-tubes, but which carry paired limbs on nearly the whole series of their trunk-segments, the foremost of these modified into sharp-fanged "poison-feet" for killing prey. There are the Diplopoda (millipedes) sometimes confused with the last named, like them elongate and many-legged, but readily distinguished by the cylindrical form of their bodies, most of the segments whereof are united in couples, so that the usually numerous legs, carried right underneath the body, seem to be arranged two pairs on one segment. Then there are the Arachnida (scorpions, spiders, mites, etc.), in which the foremost pair of developed appendages are never feelers, but seizing or piercing organs used for feeding, while there are usually not more than four pairs of legs. It is worthy of note that in Crustacea, Arachnida and Millipedes, the reproductive openings are situated far forward in the body, while in the Centipedes, as in the Insects, they are close to the tail-end.

In this brief summary of the leading arthropodan classes, stress has been laid on those characters whereby they are distinguished from insects; the characters that may be regarded as defining the latter class may now be definitely set forth.

## Class Insecta

The Insecta (or *Hexapoda*) are Arthropoda in which the segments are grouped into three regions: the head, the thorax, and the abdomen. The head carries usually a pair of compound eyes, a pair of feelers, and three pairs of jaws: mandibles maxillae, and labium; a pair of small maxillulae may also be recognizable behind the mandibles, associated with the median tongue. The thorax consists of three segments, each of which bears a pair of legs and the two hinder usually carry also each a pair of wings. The abdomen consists of eleven or fewer segments, from most of which limbs are usually absent; when present these (except in some few cases the hindmost, *cerci*) are always (in adult insects) much shorter than the thoracic legs. Limbs (*cerci* and *stylets*) usually short, are not uncommonly present at the tail end; processes of the eighth and ninth abdominal segments usually serve as accessories to the

reproductive organs whose ducts open far back on the abdomen. Insects breathe by means of branching air-tubes which open by paired spiracles on the sides of most of the body-segments. Like other Arthropoda, insects produce large eggs with a considerable quantity of yolk ; these are generally laid by the female and subsequently hatched, but in some cases they undergo development within the body of the mother, who thus gives birth to active young. When born or hatched, young insects are always without wings ; in other respects they may resemble their parents closely or they may differ from them very markedly in outward appearance. During the period of growth, which is necessarily accompanied by a series of moults, the wings are developed, the general aspect of the body remaining much the same throughout the process, or undergoing a marked transformation or metamorphosis.

The Class of the Insecta is divided into three sub-classes, which are distinguished from each other by the nature of the wing-growth.

### Sub-Class I. APTERYGOTA

These are wingless Insects in which the wingless condition is believed to be primitive. The mandibles are more like those of the Crustacea than those of other insects, and the maxillulae are well developed. Abdominal limbs are present in the adult. Transformation is slight or absent.

Three orders are included in the Apterygota.

#### Order 1. *Thysanura*

The Thysanura or bristle-tails are wingless insects with elongate feelers, an abdomen with ten segments, the hindmost of which bears a pair of prominent limbs (usually jointed *cerci*), while short unjointed paired limbs (*stylets*) are present on other abdominal segments (from the second to the ninth, inclusive, or fewer). There is a well-developed system of air-tubes. The eighth and ninth abdominal segments carry prominent reproductive processes (*gonapophyses*).

Newly-hatched Thysanura may differ from the adults in

the absence of the gonapophyses and in the absence of scales, which form a close covering to the body and limbs in most members of the order. They pass, therefore, through a slight but definite transformation.

### Order 2. *Protura*

The Protura are very small wingless insects without feelers or cerci. The jaws are modified into piercers and the creatures feed by suction. The abdomen has a pair of short unjointed limbs on each of the first three of its eleven segments.

### Order 3. *Collembola*

The Collembola or spring-tails have short feelers with four or six segments, no compound eyes but groups of ocelli (usually eight on each side of the head), the mouth inpushed so that the jaws seem retracted within the head. The abdomen consists of six segments only, the limbs of the first segment are united to form an adhesive ventral tube, those of the third are minute, forming a catch (*retinaculum*) which holds the spring consisting of the limbs of the fourth abdominal segment. The air-tube system is usually wanting, breathing being carried on through the thin body-wall.

Young spring-tails closely resemble their parents and undergo no transformation.

## Sub-Class II. EXOPTERYGOTA

The great majority of these insects are winged ; the wingless condition of some is clearly secondary. Wing-rudiments appear on the second and third thoracic segments at an early stage in the life-history, and increase in size until the penultimate stage, after which wings become fully developed in a short time so that they can be used for flight. The newly-hatched young of these insects may resemble their parents very closely, except for the absence of wings (ametabolous insects) or may differ so markedly from them that they have to undergo a considerable transformation (hemimetabolous

insects). Most Exopterygota are active and take food in all stages of the life-history.

Eleven living orders of insects are included in this sub-class.

### Order 4. *Dermaptera*

The Dermaptera have biting mandibles, fairly prominent maxillulae, typical maxillae and a labium of which the parts of the component appendages are distinctly recognizable. The forewings are modified into short, firm covers beneath which the delicate membranous hindwings can be folded when at rest. Many Demaptera are wingless. The tenth abdominal segment carries a pair of limbs which are usually strong and unjointed forming a forceps (*Forficulidae* or earwigs). In the wingless, parasitic *Hemimeridae* these limbs are jointed cerci. The genital ducts (either paired, or single through the suppression of one) are entirely mesodermal in origin.

Young members of this order resemble their parents very closely, but in some earwigs, the tail-appendages of the newly-hatched insect are jointed, becoming transformed into forceps after the first moult.

### Order 5. *Orthoptera*

The Orthoptera (cockroaches, stick and leaf insects, grasshoppers, crickets, etc.) have biting mandibles and reduced maxillulae; maxillae and labium are as in the Dermaptera. The forewings are elongate, relatively narrow and firm in texture, the more delicate and ampler hindwings being folded beneath them when at rest. The abdomen has jointed cerci on the tenth segment. The outer genital ducts, as in the vast majority of insects, are unpaired and ectodermal in origin, lined with chitin. The female's ovipositor is well and typically developed.

Young Orthoptera resemble their parents very closely except for the absence of wings.

### Order 6. *Plecoptera*

The Plecoptera (stone-flies) have the same general characters as the Orthoptera, but the mandibles are often much reduced

in the adult, and there is only slight difference in texture between the fore- and hindwings.

These insects develop from aquatic nymphs which live submerged in streams and breathe by means of tufted thoracic gills. In some stone-flies these gills persist in a reduced condition in the winged adult.

### Order 7. *Isoptera*

The Isoptera (including termites or " white ants ") have jaws like those of the Orthoptera, but the fore- and hindwings are very closely alike and the cerci very short. The vast majority of these insects are wingless (" workers " and " soldiers "). The form of the individual insect within the same species may vary to such a degree as to call for some considerable change of form during growth.

### Order 8. *Corrodentia*

The Corrodentia (booklice and allies) have elongate feelers, biting mandibles, maxillae with the lacinia narrow and elongate forming a characteristic " pick," wings (when present) delicate, the forewings longer and broader than the hindwings, and the abdomen without cerci.

Young booklice resemble their parents in general form, but during the growth of the winged insects, the prothorax becomes relatively reduced.

### Order 9. *Thysanoptera*

The Thysanoptera (Thrips) have short feelers, slender piercing mandibles, and maxillae in which a piercing lacinia is present on the left side only. Both maxillae and labium bear palps. The insects feed by suction. Wings, when present, are very narrow, relatively long, and fringed with fine bristles. The abdomen is narrow and elongate and the female has a well-developed ovipositor. Cerci are absent.

Young Thrips resemble the adult in general form, but the last nymphal stage, with prominent wing-rudiments, is quiescent (so-called " pupa ").

### Order 10. *Mallophaga*

The Mallophaga (biting-lice) have short feelers, reduced eyes, biting mandibles, palps on the maxillae, and, in some families, on the labium. They are wingless parasites with the hinder thoracic segments imperfectly distinguished, and the feet adapted for clinging to the feathers or hairs of their hosts. Cerci are absent.

Young biting-lice resemble their parents very closely.

### Order 11. *Anoplura*

The Anoplura (lice) are wingless parasites with short feelers and a tubular, piercing and suctorial mouth in which the typical insectan jaws can be hardly recognized. The legs with strong one-clawed feet are adapted for clinging to the host's hair. The abdomen bears no cerci, but the adults have prominent genital armature.

Except for the absence of these last-named structures, young lice resemble their parents very closely.

### Order 12. *Hemiptera*

The Hemiptera are insects in which the mouth is adapted for piercing and sucking by the modification of mandibles and maxillae into elongate, needle-like piercers which work to and fro in a groove on the front face of the long, jointed labium (rostrum or " beak "). The feelers have comparatively few segments ; the wings are variable in structure and development, the abdomen is without cerci, but there is a typical, often prominent ovipositor. Two well-distinguished sub-orders may be recognized.

#### Sub-Order i. *Heteroptera*

The Heteroptera or bugs have the base of the rostrum placed well forward, the forewings of firmer texture than the hindwings, but usually with a well-marked membranous apex, the wings lying flat on the back when at rest.

Young Heteroptera resemble their parents in general

form, pass through no marked transformation, and, like most exopterygote insects, are active throughout life.

### Sub-Order ii. *Homoptera*

The Homoptera (cicads, froghoppers, snowy-flies, aphids, coccids, etc.) have the rostrum inserted far back close to the bases of the forelegs. The wings of both pairs are often alike in texture and are held vertical or sloping when at rest.

Young Homoptera may resemble their parents closely (aphids) or may differ from them markedly (cicads, coccids). In the latter case there is usually a quiescent final nymph-stage (so-called " pupa ") in the life-history.

### Order 13. *Ephemeroptera*

The Ephemeroptera (mayflies) are delicate insects with short feelers ; in the adult the jaws are reduced to mere vestiges so that feeding is impossible. The wings are membranous with complex netted nervuration, the forewing much longer and broader than the hindwing. The elongate abdomen bears long paired cerci, and often also a median tail-filament. The paired genital ducts are entirely mesodermal.

Mayflies have aquatic larvae with the crustacean type of mandible, prominent maxillulae, and in addition to the tail cerci, a series of paired abdominal appendages which are modified into gills. The mature nymph on leaving the water becomes changed into the sub-imago—an instar with wings capable of flight, but having to undergo a final moult before the true imago is revealed.

### Order 14. *Odonata*

The Odonata (dragon-flies) are strong, predaceous insects, with short feelers, very prominent eyes, and formidable biting mandibles and maxillae. The legs thrown forward under the mouth serve as a fly-trap and the stiff, glassy wings, incapable of folding are very similar in the two pairs. The elongate abdomen has short, unjointed cerci and prominent reproductive processes at the tail end.

Dragon-fly larvae are aquatic, breathing by means of an air-tube network in the wall of the hind-intestine, or by cerci, in addition to a median tail-filament, transformed into tracheal gills at the tail end. The labium is modified into a protrusible seizing organ (" mask "). The mature nymph leaves the water and becomes changed into the winged adult.

## Sub-Class III. ENDOPTERYGOTA

The great majority of these insects are winged, the wingless condition of some being clearly secondary. The newly-hatched young is always a *larva* differing more or less markedly from its parent, and no trace of wings is usually to be seen externally through the various stages of larval life, because the wing-rudiments formed in the second and third thoracic segments at an early stage in the life-history, grow in pouches pushed in from the body-wall, so that they are not covered by cuticle. The legs and other organs of the winged adult are similarly formed in the larva from inpushed imaginal discs or buds. These, pushed out during the last larval stage, become revealed in the *pupa*—a usually quiescent instar which does not feed. During the pupal period there may be a greater or less degree of internal reconstruction in the insect in preparation for the adult condition.

Nine orders of living insects are included among the Endopterygota.

### Order 15. *Coleoptera*

The Coleoptera (or beetles) have biting mandibles, maxillae with all typical parts, and a labium in which the fusion between the two component appendages is close. The prothorax is freely movable on the segments behind. The forewings, hard and firm in texture, are modified as sheaths (*elytra*) beneath which the membranous hindwings can be folded when at rest. (Many beetles have these hindwings so far reduced as to be incapable of flight.)

The larvae of beetles show great variety of form, ranging from active, armoured, long-legged *campodeiform* grubs to soft-cuticled *eruciform* larvae in which legs are short or absent.

In the life-history of some beetles, the former type is succeeded by the latter (*hypermetamorphosis*). Beetle pupae have the wings and appendages not fixed to the body ("free" type of pupa).

### Order 16. *Neuroptera*

The Neuroptera resemble beetles in the nature of their jaws, but have the wings of the two pairs membranous and closely similar in their nervuration, a series of short nervules from the sub-costal nervure to the costa being characteristic. There are no cerci on the last abdominal segment.

The larva is long-legged and well-armoured, the pupa is of free type and the pupal wing has a full series of tracheal trunks. Two sub-orders may be recognized.

#### Sub-Order i. *Megaloptera*

The Megaloptera (including alder-flies, snake-flies, etc.) have larvae with biting jaws essentially like those of the adult.

#### Sub-Order ii. *Planipennia*

The Planipennia (lace-wing, golden-eye and ant-lion flies) have larvae with mandibles and maxillæ specially modified for sucking liquids (usually the juices of other insects).

### Order 17. *Mecoptera*

The Mecoptera (scorpion-flies) have the head prolonged into a beak at the tip of which the biting jaws are situated. The wings of both pairs are membranous with a less specialized nervuration than that of the Neuroptera. The abdomen is elongate, the male with prominent genital armature, the female with an elongate ovipositor ; cerci are present on the last abdominal segment.

Scorpion-flies have eruciform larvae with biting mandibles, three pairs of strong thoracic legs, and eight pairs of abdominal prolegs some of which may be jointed and clawed. The pupa

is free, its wings possessing only radial and median tracheal trunks.

### Order 18. *Trichoptera*

The Trichoptera (caddis-flies) have no mandibles, the maxillae and labium being adapted for sucking. The hairy wings are membranous, the forewings being long and narrow, the hindwings shorter and broad, with a folding area; there is a full set of longitudinal nervures in both wings but cross-nervules are few. Abdominal cerci are absent.

The larvae ("caddis-worms") of Trichoptera are aquatic. They have strong biting mandibles and well-developed, clawed thoracic legs. The body-cuticle is comparatively feeble, as these larvae are sheltered in cases which they construct by spinning together fragments of plants, stones, etc. The "free" pupa is provided with strong biting mandibles; its wing has only two tracheal trunks: the radial and a cubital or an anal.

### Order 19. *Lepidoptera*

The Lepidoptera (moths and butterflies) have (except in one most primitive group) no mandibles and no maxillary laciniae, the maxillary galeae long and flexible forming a sucking trunk or proboscis. The scale-covered wings have a nervuration mainly longitudinal. The abdomen has no cerci, and the genital armature though well-developed is inconspicuous.

The larvae of Lepidoptera are of eruciform type (caterpillars), with short feelers, strong biting mandibles, jointed thoracic legs and abdominal prolegs (five or fewer pairs) usually unjointed and with terminal hooks or spines. The pupa is very exceptionally "free" and mandibulate; usually it is more or less obtect. The pupal wing has a complete set of tracheal trunks.

Two sub-orders of the Lepidoptera may be recognized.

#### Sub-Order i. *Homoneura*

In this more primitive section the hindwing has, like the forewing, five radial nervures; here are included the

families with free and mandibulate pupae, and also some with the pupa non-mandibulate and partly obtect.

### Sub-Order ii. *Heteroneura*

In this section, including the great majority of the order, the hindwing has only one radial nervure or two (radial trunk and radial sector), while the forewing has the normal five. The pupa, more or less obtect, is always non-mandibulate.

## Order 20. *Diptera*

The Diptera (two-winged flies) have the labium highly modified as a sucking organ; mandibles may be absent or present as piercing-organs. Parts of the maxillae may also be modified as piercers; maxillary palps are present, labial palps absent. The prothorax is of small extent and closely united with the large mesothorax; the membranous forewings are well developed for flight, while the hindwings are reduced to short, clubbed equilibrating organs. The abdomen carries cerci, which with the genital armature and hinder segments generally are often concealed.

The larvae of Diptera are eruciform or vermiform, all without true thoracic legs, but prolegs may be present on some of the segments. The pupa is free or obtect, the pupal wing has the tracheal system reduced.

Two sub-orders of Diptera have been recognized and are distinguished by the nature of the early stages.

### Sub-Order i. *Orthorrhapha*

In this section (including the various families of midges and gnats, crane-flies, black-flies, breeze-flies and others) the larva has a distinct head with mandibles. The cuticle of the pupa splits lengthwise, as is usual in insects, to allow the emergence of the imago.

### Sub-Order ii. *Cyclorrhapha*

In this section (including the hover-flies, the house-fly and blue-bottle group of families, the bot-flies, etc.) the

larva is a headless maggot with mouth-hooks. The last larval cuticle hardens to form a *puparium* from the front end of which a round lid splits off to allow the escape of the imago.

### Order 21. *Aphaniptera*

The Aphaniptera (fleas) are laterally compressed, wingless insects, parasitic in the adult state on vertebrates whose blood they draw by means of highly-specialized elongate piercing and sucking jaws, both maxillary and labial palps being developed.

The larvae of fleas are of an eruciform, legless type with well-developed head provided with biting mandibles. The pupa is free

### Order 22 *Strepsiptera*

The Strepsiptera are minute insects parasitic (except the free-flying males) on various Hymenoptera and Hemiptera. The male has complex feelers, slender mandibles and reduced maxillae, a very short prothorax and elongate metathorax; the forewings are club-shaped balancing organs, the hindwings broad and membranous with simple longitudinal nervures and no cross-nervules. The abdomen has ten segments with prominent genital armature. The female has all the appendages vestigial and is wingless; the head is fused with the thoracic segments and the abdomen shows normal segmentation; she lives within the body of the host insect. There is a remarkable hyper-metamorphosis. Active campodeiform larvae with clawless sucker-feet emerge from the front end of the mother's body, and enter the larva of the host, where they become legless grubs with degenerate head. The free pupa is enclosed in a puparium, whence the female never completely emerges. In some males a pre-pupal stage with wing-rudiments can be recognized.

### Order 23. *Hymenoptera*

The Hymenoptera have typical biting mandibles and a suctorial labium, both pairs of wings usually developed,

membranous, the forewing larger than the hindwing, which is attached to it during flight by a row of hooks along the costa. The first abdominal segment is annexed to the thorax. Cerci are present, and the female's ovipositor is strongly developed.

The larvae of Hymenoptera are of the eruciform type with well-developed, mandibulate head. The pupa is " free ".

Two sub-orders of Hymenoptera are recognized.

### Sub-Order i. *Symphyta*

The Symphyta (saw-flies) have no constriction at the base of the abdomen. The larva is usually a caterpillar with three pairs of thoracic legs, and seven or eight pairs of abdominal prolegs without hooks or spines.

### Sub-Order ii. *Apocrita*

The Apocrita (gall-flies, ichneumon-flies, wasps, bees, ants) have a marked constriction (" waist ") behind the first abdominal segment. The larva is always a legless grub.

CHAPTER VII

# GROWING INSECTS AND THEIR SURROUNDINGS

IN the earlier chapters of this volume some account has been given of the growth and accompanying transformations of a number of insects of various orders, so as to illustrate varying degrees of outward and inward change during development, and to display the greatly differing modifications of form assumed by different insect larvae. In these descriptions, some attention was necessarily paid to the manner of life of these young insects, and it was seen how their structure is adapted to the surroundings in which they have to live and feed. It may now be advantageous to give further examples of the variety of form displayed by insects during their period of growth, with especial reference to this important question of environment. The development of any animal from the fertilized egg to the close of life may be considered as determined by the factors and tendencies inherited through an immensely extended line of ancestry, and by the influences brought to bear on the individual through the surroundings in which it has to live. A discussion as to the detailed operation and the relative importance of heredity and environment in the moulding of the organism would be beyond the scope of this book, but a study of insect transformation from the environmental point of view provides many facts, highly interesting and suggestive with regard to these problems, which have been, and still are, the subject of eager discussion among students of living nature.[1] To the biologist the term " environment " or " surroundings " suggests a survey of the conditions of a creature's life in the widest sense—where it lives, how it feeds, its experiences and activities, what drawbacks in its life-relations it may have to overcome, what other living creatures are its competitors, or maybe its deadly

[1] J. Arthur Thomson : " Heredity ". London, 1919.

enemies, how it obtains against them some measure of protection ; all these aspects of the surroundings demand consideration. Insects, on account of their immense numbers in species and often in individuals, and the great variety in details of structure which they display, are admirably suited as the subjects for such a comprehensive study. We are thus concerned with insects in relation to their surroundings during the period of growth and change.

Among the Exopterygota it frequently happens that the young growing insect, resembling closely its parents in most features of bodily structure, lives and feeds in much the same way. Such is the case for example with grasshoppers, cockroaches, lice, bugs, green-fly, and many other groups—the life-history of which has been reviewed in previous chapters. But in other Exopterygota, and in almost all orders of the Endopterygota, the mode of life of the larva differs greatly from that of the imago, and this sharp distinction of habit and behaviour accompanying the distinction in structure during the successive periods of an insect's existence is a striking and suggestive feature in the developmental history of the class.

We have already traced the main features in the life-history of dragon-flies (pp. 39–52) and mayflies (pp. 91–7). These afford well-known examples of insects whose larval stages are passed under water, and such a marked divergence between the surroundings of the adult insect and those of its young is worthy of attention. Insects, as a class, are pre-eminently aerial creatures, stamped as such by their power of flight and the system of complex branching air-tubes by means of which they breathe. Yet many insects live habitually in water during the perfect stage—several families of beetles, for example, besides such groups of bugs as the water "scorpions" and water "boatmen". Without exception these insects that are aquatic in the winged state breathe atmospheric air, having some provision for carrying down with them below the surface a supply of air, stored for example beneath the wing-cases of many water-beetles, or for keeping in touch with the atmosphere by means of prolongations of the body, such as the tail-processes of the water-scorpion, thus ensuring a sufficient supply of fresh air to the tracheal system. Such arrangements

emphasize the fact that insects—even though they live in water—belong essentially to the air, and most of them can, on occasion, rise from their watery homes and indulge in flights of considerable extent.

But in the dragon-flies and mayflies we have to do with insects that are typically aerial in the winged state, while their larval and nymphal stages are aquatic. These growing forms have, as we have seen, some provision for breathing the air dissolved in water—the mayfly grubs by their paired series of abdominal appendicular gills, the dragon-fly larvae by the network of air-tubes branching over the thin wall of the hind-intestine or by the terminal gills modified from the tail appendages. Such modifications of insect larvae for aquatic life[1] may be seen in different families and orders; reference has already been made to the stone-flies (Plecoptera) whose larvae (see pp. 76–7) have tufted thoracic gills and to the caddis-flies (Trichoptera) whose well-known case-inhabiting grubs (see pp. 121–3) have thread-like abdominal gills. Many examples of similar larval adaptation for life under water are afforded by certain families of the Diptera, and to these attention may now be profitably directed.

The delicate midges of the genus *Chironomus*[2] often fly in swarms on summer evenings in the neighbourhood of water; they have relatively long legs and abdomen, and the males possess beautifully plumose feelers. The female, distinguished by much simpler feelers, lays in water numerous eggs embedded in a gelatinous substance which assumes the form of a long string or cord; the eggs lie in a tube which runs a spiral course near the surface of this gelatinous cord, and they may approach a thousand in number in one laying. The larva of a Chironomus (Fig. 100 *b*) is a narrowly elongate grub, its distinct head bearing short segmented feelers and strong toothed mandibles which work obliquely backwards, not transversely across the mouth. The first thoracic and the last abdominal segments bear each a pair of hooked prolegs, and the special breathing-organs are found on the last and the penultimate abdominal

[1] L. C. Miall: "The Natural History of Aquatic Insects". London, 1895.

[2] L. C. Miall and A. R. Hammond: "The Harlequin Fly". London, 1900. J. G. Needham and others: "Mayflies and Midges of New York". Albany, New York, 1905.

segments in the form of thread-like or finger-like "blood-gills" (*g*). Through the thin walls of these delicate outgrowths of the grub's body gaseous exchange goes on between the contained blood and the air dissolved in the surrounding water, oxygen being absorbed and the products of combustion eliminated. Many Chironomus larvae are bright red in colour, being known as "blood-worms". They form tubular shelters at the bottom of the ponds and ditches which they inhabit, by fastening together small fragments of soil. The grub may often be seen thrusting its hinder end out of this protective

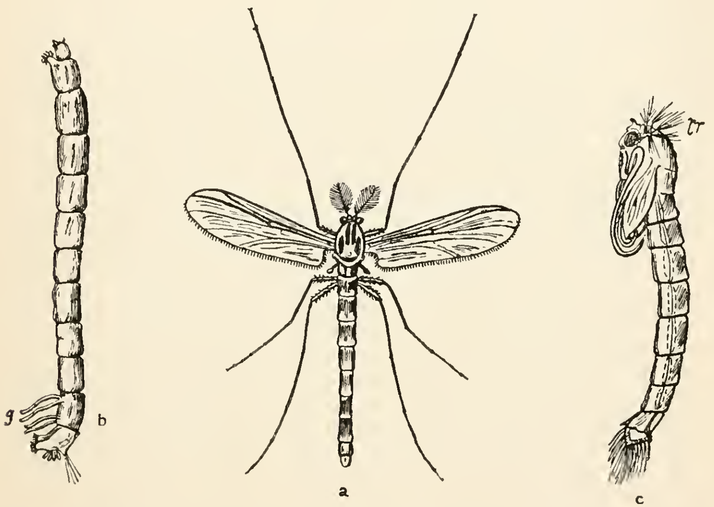



FIG. 100.
*a*, Harlequin Midge (*Chironomous*), male; *b*, larva (*g*, gill-filaments); *c*, pupa (*tr*, tracheal gills). × 4. After Johannsen, *Bull.* 86, *New York State Museum.*

sheath and waving its delicate gill-processes vigorously in the water, so as to facilitate the absorption of the dissolved oxygen. Even while remaining within the tube it practises a wave-like movement of the body, which keeps fresh water-currents constantly bathing it. This action suffices for ordinary needs, but sometimes a richer supply of oxygen becomes a necessity; then it leaves its tube altogether, rising to the surface region of its native pond or ditch, where the water is less poorly aerated than in the depths. The red colouring-matter of these "blood worms" is similar to the haemoglobin of our

own blood, a respiratory pigment which has the power of seizing oxygen and holding it in a loose combination so that it may be given up to the tissues of the body, as they need it for the support of the combustion-processes that are always going on in living matter. The head of the worm is also frequently seen to emerge from the sheltering tube, the feelers being directed to various points, and the jaws working strongly to seize and break up the particles of decaying plant-substances which serve these larvae for food.

With the assumption of the pupal stage it is interesting to observe a change in the position of the breathing organs. Like the larva, the pupa (Fig. 100 *c*) lives under water, and a flattened expansion of the tail-segment gives to it a certain power of movement. At the front end of the thorax, just behind the head, are situated a pair of outgrowths. commonly in the form of delicate-branching, tufted filaments, but sometimes simply tubular, or clubbed. These, like the tail-processes of the larva, are gills by means of which the insect in this stage of its life-history obtains its supply of oxygen ; but, unlike the larval organs, they contain prolongations of the air-tube system, and are therefore tracheal gills. There is a beautiful provision, by the degeneration of the very narrow air-tubes at the bases of these organs, for their rupture at the close of the pupal period, so that they are shed with the pupal cuticle and not remade for the aerial imago which will not need them.

In the larvae of some members of the Chironomid group, it is interesting to observe that special breathing organs, like those just described, are absent, and the exchange of gases goes on through the thin body-wall generally. Such is the condition in the larva of the interesting little marine midges (*Clunio*) with their feebly-winged males and wingless females. The Clunio grub, essentially like that of a Chironomus without special gills, feeds on green seaweeds and, visible only during the low spring-tides, must be submerged in salt water for the greater part of its life.

Midges of the Chironomus group pass their larval existence in ponds, ditches or sluggish streams. The allied sandflies (*Simuliidae*), whose females, though of small size, are often voracious and even dangerous blood-suckers, have larvae

(Fig. 101 *a b*) that live in swift clear streams, and these little blackish grubs are said to die in a few hours if transferred from their native torrents into still water. They build no tube or other shelter, but spend much of their time attached to water-plants or submerged stones by means of a sucker-process at the hinder end of the body, which is probably formed by the union of a pair of tail prolegs. Similarly the prolegs on the prothorax, which in the Chironomus larva retain their normal paired condition, are in the Simulium larva, joined together to form

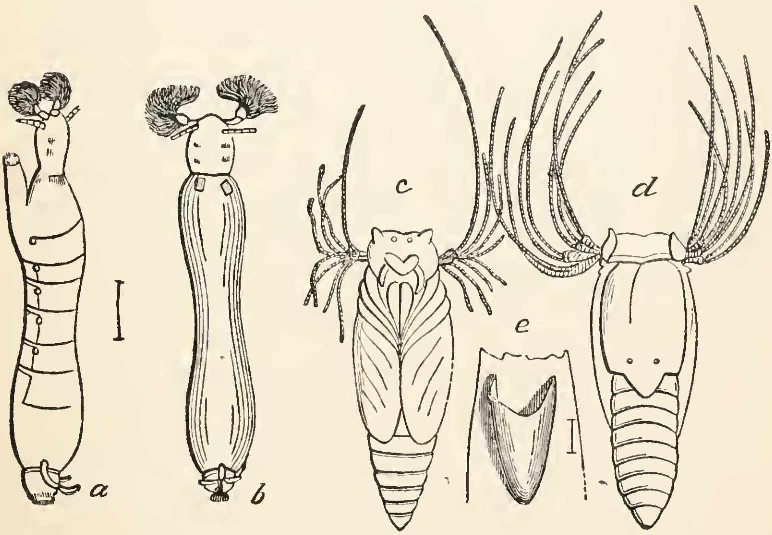



FIG. 101.
*a*, Larva of Sandfly (*Simulium*), side view ; *b*, dorsal view ; *c*, Pupa (ventral view) ; *d*, dorsal view. × 7. *e*, cocoon. × 4. From Osborn, *U.S. Dept. Agric. Ent. Bull.* 5, after Verdat.

a short median limb, so that this grub can move about after the manner of a leech or a " looping " caterpillar. Besides its short feelers and the usual series of jaws—mandibles, maxillae and labium—the head of the sandfly larva is provided with a pair of beautifully fringed plates, known as the " fans " or " brushes ". These serve to waft into its mouth the microscopic plants and crustacea which furnish its food-supply. In the rush of the well-aerated water that it inhabits, the larva needs no special breathing organs. The salivary secretion, discharged from the mouth, forms a silken thread, and the

grubs are thus able to construct a labyrinth of intersecting lines about their resting-places, so that they can move rapidly from spot to spot without risk of being washed away by the strong currents which suit the requirements of their lives. Clinging to the thread by means of the fine hooks on their prolegs, they move along the line with ease and safety in the direction of the water's flow, while the anchorage thus afforded enables them to make way against the current surely if slowly.

The pupa (Fig. 101 *c d*) of Simulium has, like that of Chironomus, paired filamentous gills on the prothorax. It is protected by a flask-shaped cocoon (Fig. 101 *e*) of closely-interlaced silken threads spun by the larva before its final moult. The abdominal segments are provided with rows of hooks which anchor it firmly while the head and the waving thread-like gills project from the front end. It may seem difficult to imagine how from this submerged pupa the midge can make its way into the upper air. Nearly a century ago, however, it was discovered[1] that, through the action of the gills, air accumulates beneath the pupal cuticle so that when the latter slits, a small bubble which necessarily surrounds the fly rises to the surface, where bursting, it liberates the winged insect. This can run upon the surface of the water and climb up the aerial part of some aquatic plant ; thence, as soon as its wings are fully expanded and dried, it takes its short flight.

The air-bubble that surrounds the emerging Simulium, and the running of the little midge over the surface of the water may serve to introduce a subject of great interest in the surroundings of aquatic insect larvae : their relation to the surface-film. Many adult insects, such as pond-skaters and various flies run over the surface of water which they depress without breaking, so that they never get wetted. Most inquiring people know that by careful manipulation, a steel needle may be supported by the surface-film of water in a glass, though the breaking of the film will cause the needle immediately to sink. This tensile property of a water-surface, useful to the adult insects just mentioned that live above it, is also most valuable to many insect larvae that live beneath it, because

[1] G. J. Verdat : "Memoire pour servir a l'Histoire des Simulies" *Naturwissens. Anz. d. allgemein. Schweiz. Gesellsch.* 1822.

by means of it, they can get into direct touch with the atmosphere and do not require special gills for breathing dissolved air. This mode of respiration has already been mentioned in connexion with the larva of the carnivorous water-beetles (*Dyticus*, see pp. 101–2). We may now turn to certain larvae of Diptera that are able thus to draw on the atmospheric source for their needed oxygen.

In an earlier chapter (pp. 130, 133) we saw that many dipteran larvae have the functional spiracles restricted to a pair at the hinder end of the body; such an arrangement is advantageous for a maggot living buried in some decaying organic substance. This position of the spiracles is clearly a good adaptation for enabling larvae living submerged in water to get into contact with the air by thrusting the tail-region up to the surface. As an example of such an adaptation we may take the familiar larva of a common gnat (*Culex*). Gnats—or mosquitoes as they are often called—are notorious insects on account of the unpleasant habit of blood-sucking practised by their females which are provided with formidable lancet-like mandibles and maxillae, capable of piercing the skin and giving the insect's suctorial labium access to blood. The female gnat (Fig. 102 *a*) lays her eggs on the surface of stagnant water, the eggs being associated in a small mass—known as the " egg-raft " because it floats—each egg (*b*), with its long axis vertical, opening by a little circular lid at the lower end so that the newly-hatched larva dives at once into the water. The larva (Fig. 102 *c*) has a relatively large head with short feelers, prominent fringed " combs " or " brushes ", like those of the Simulium larva described above, which sweep particles of food into the mouth, and the typical insectan mandibles and maxillae. The thorax is very broad, its three constituent segments not clearly distinguishable. The abdomen is narrow and sub-cylindrical, its terminal segment, through which the intestine opens, bearing long bristles and stiff plate-like processes. From the last segment but one diverges a dorsal cylindrical outgrowth (*sp*) through which the tracheal trunks run, a spiracular siphon with the apertures of the air-tubes at its tip, guarded by a group of little, pointed processes which can be brought together at their slender apices or spread out somewhat like petals of a flower. The gnat-larva swims

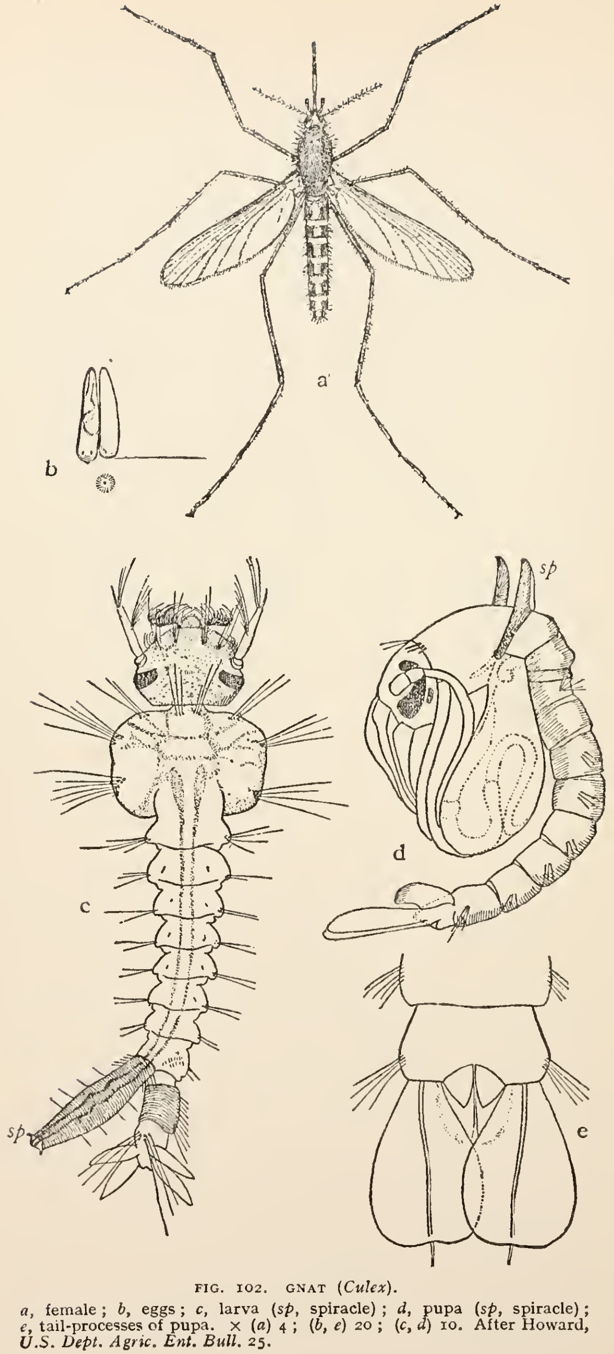



FIG. 102. GNAT (*Culex*).

*a*, female ; *b*, eggs ; *c*, larva (*sp*, spiracle) ; *d*, pupa (*sp*, spiracle) ; *e*, tail-processes of pupa. × (*a*) 4 ; (*b*, *e*) 20 ; (*c*, *d*) 10. After Howard, *U.S. Dept. Agric. Ent. Bull.* 25.

through the water by undulating movements of its abdomen, often in constant motion diving to the bottom of its native ditch or rising to the surface. When it rises it can bring together the points of the processes of its spiracular siphon, and it is thus capable of piercing the surface-film (Fig. 104 *a*). Then, separating these points, it exerts a pull on the tensile surface so that a little cup-like depression is formed from which the siphon and indeed the whole larva is, as it were, suspended, so that its air-tube system is open to the atmosphere ; it takes in air through the tail-spiracles directed upwards while it can feed through the downwardly-directed mouth. After thus hanging from the surface-film for a time, the larva closes the cup by bringing together the points of its processes and releases itself ; then with a supply of fresh air in its tracheal system, it dives and moves again with vigorous graceful flexions of its abdomen through the deeper layers of the ditch-water where food is more abundant than near the surface.

Among the details already given of the aquatic larva and pupa of the midge Chironomus it will be remembered that the gills of the larva are at the hinder end of the abdomen while those of the pupa are on the prothorax. A closely similar change in the position of the breathing organs is seen in the transformations of Culex. The pupa (Fig. 102 *d*) of the gnat, with its relatively very large, rounded thorax and its elongate, freely-jointed abdomen with terminal fin-like processes (*e*), is capable of a considerable degree of movement, and is far less passive in habit than are most insectan pupae. Like the larva it breathes atmospheric air, but unlike the larva its spiracles (*sp*) are on the prothorax at the end of a pair of elongate tubular or trumpet-shaped outgrowths, so that the pupa hangs from the surface film with the head and tail ends both pointing downwards and the dorsal thoracic region uppermost. This arrangement has drawn admiring comment from students of insect transformations both in early and modern days. For this dorsal thoracic region, close to the surface, is the portion of the pupal cuticle that splits open to allow the emergence of the gnat, and the elongate feelers, jaws, legs, wings, and abdomen of the imago have to be withdrawn from the pupal structures wherein they have developed towards this region so as to be extricated from the cast pupal envelope. And the

result is that the newly-emerged gnat finds itself on the surface of the water, the empty pupal husk which floats often serving it as a raft-like support on which it can rest and dry its wings.

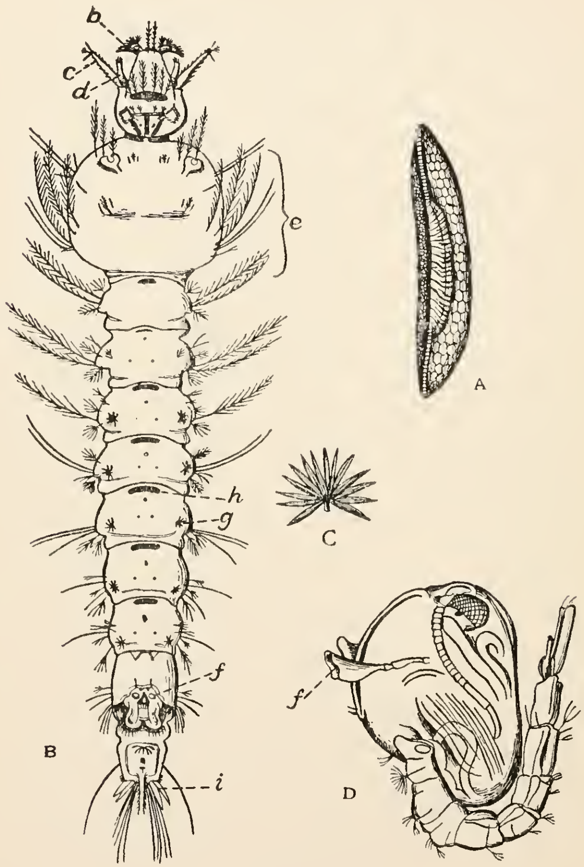



FIG. 103.

A, Egg of *Anopheles*. × 40. B, Larva, dorsal view (*b*, brush; *c*, feeler; *d*, maxillary palp; *e*, thorax; *f*, spiracle; *g*, stellate hairs; *h*, abdominal terga; *i*, anal papillae). × 10. C, a stellate hair, × 70. D, pupa (*f*, spiracle). × 10. After Nuttall and Shipley, *Journ. Hyg.* I.

Less abundant in these countries than the Culicine gnats are the Anophelines[1]—members of the same family but distinguished by the very elongate maxillary palps of the

[1] G. H. F. Nuttall and A. E. Shipley: "The Structure and Biology of Anopheles". *Journ. Hygiene.*, Vol. I. 1901.

blood-sucking females. Certain species of these anopheline mosquitoes are notorious and of very great importance because they serve alternately with human beings as hosts of microscopic animal parasites which, in man, give rise to forms of malaria and other dangerous diseases. The larva of Anopheles (Fig. 103) is of the same general build as that of Culex, but the spiracles (*f*), instead of being situated at the end of a long siphon are found occupying a rather prominent area on the dorsal aspect of the eighth abdominal segment. The Anopheles larva is to be seen lying horizontally suspended, by pairs of beautiful stellate hairs on the dorsal aspect of five of the abdominal segments, from the surface film, which is broken immediately over the spiracular region so as to bring the cavity of the larval tracheal system into continuity with the atmosphere (Fig. 104 *c*). While the larvae of culicine mosquitoes —many of which carry the germs of dangerous human maladies, as the Anophelines do, in warm and tropical countries—live in ditches, in cisterns, or in the water accumulated in neglected pots and cans, the anopheline larvae are found rather in clear ponds, in swamps, and in slow-running streams in which there is a fairly abundant growth of aquatic plants. The important and fascinating subject of the relation of such blood-sucking-insects to human diseases is beyond the scope of this book, but it may be pointed out how closely knowledge of the insect life-histories bears on practical measures of "protective medicine." The incidence of certain diseases has been immensely reduced in many tropical districts by altering the environment so as to render it unsuitable for the disease-bearing insects to breed in ;[1] the spread of knowledge of these life-histories has set men draining swamps, covering cisterns with lids, and ditches and puddles with a film of oil impenetrable by the gnat larvae, clearing away old cans and vessels, wherein stagnant water may accumulate, from the neighbourhood of settlements. The question of the surroundings of growing insects has much to do with human life and industry ; it is doubtful if without a drastic change in the surroundings of the Canal Zone across the Isthmus of Panama, whereby the number of mosquitoes was immensely reduced, that famous waterway could ever have been completed.

[1] R. Ross : "Mosquito Brigades, and how to organize them". London, 1902.

The pupa (Fig. 103 D) of Anopheles resembles, in its main features, that of Culex. The respiratory "trumpets" (*f*) on the prothorax are jointed, and strongly expanded at their free ends; it has been observed that when the pupa leaves the surface it often carries down with it a small air-bubble attached

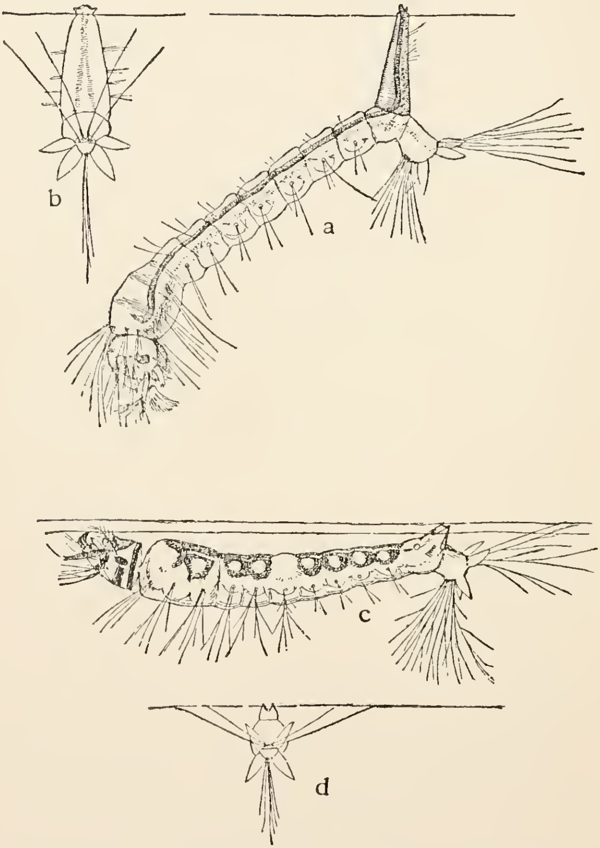



FIG. 104. POSITION OF LARVAL *Culex* (*a*, SIDE VIEW, *b*, END VIEW) AND *Anopheles* (*c*, SIDE VIEW; *d*, END VIEW), WHEN BREATHING AT SURFACE OF WATER. × 10.
After Howard, *U.S. Dept. Agric. Ent. Bull.* 25.

to the opening of each. This pupa swims actively by means of rapid strokes of its flexible abdomen which carries a pair of fin-like flaps at the hinder end.

It may be remembered that a change in the position of the functional spiracles from the tail of the larva to the prothorax

of the pupa, similar to that characterizing the midges and gnats just described, is found in the life-history of the blue-bottle and the whole group of the muscoid flies. Some of the maggots of these insects are adapted for life under water, and the allied family of the *Syrphidae* affords an excellent and well-known example of such adaptation in the curious "rat-tailed" maggots

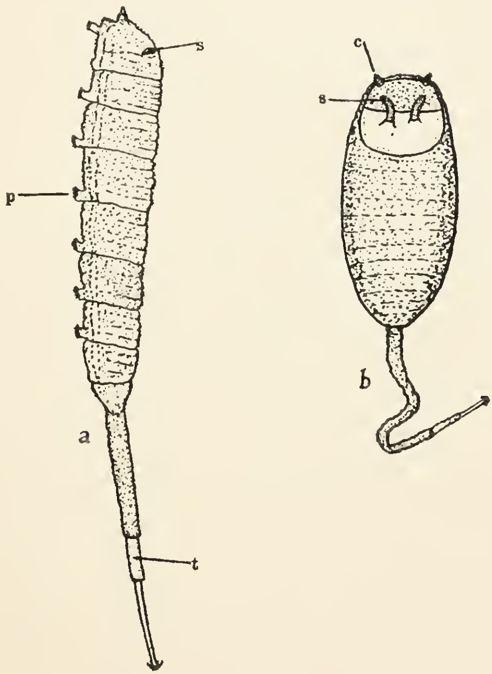



FIG. 105.
*a*, Larva ("Rat-tailed Maggot") of Drone-fly (*Eristalis*), side view (*s*, anterior spiracle; *p*, proleg; *t*, spiracular tail region); *b*, puparium of *Eristalis*, dorsal view (*s*, spiracle; *c*, anterior horn). × 2½.

(Fig. 105) of the drone-flies (*Eristalis*). These insects resemble bees in their hairy bodies and the manner of flight; they may be seen commonly in gardens hovering over flowers. Among the maggots of the Syrphidae there is a tendency for the spiracles at the hinder end of the body to be situated at the tip of prominent outgrowths; and in the remarkable life-relations of the rat-tailed maggot we see the advantage resulting from an extreme development of this tendency. This larva is an

elongate sub-cylindrical maggot, headless like all its tribe, but with seven pairs of ventral prolegs along the body ; the cuticle is rather closely covered with minute spines presenting thus a roughened aspect. From the hinder end projects the long "rat-tail"—a flexible outgrowth of the body into which the tracheal trunks are prolonged, and having a more slender and delicate distal region which can be telescoped into the thicker proximal portion, or thrust out so as to reach the surface film while the body of the maggot remains deeply submerged in water. At the extreme tip of this spiracular tail is a circlet of fine sharp spines by means of which the surface film is caught and depressed, connexion being established between the atmosphere and the maggot's air-tube system. Thus obtaining contact with the pure upper air, the larva of Eristalis is able to live submerged in the foulest liquid where it finds abundant organic food-supply. Ditches containing "retting" flax, waters heavily contaminated with sewage, even the fluids resulting from the decomposition of large animal carcases have been known to serve as suitable surroundings for the development of rat-tailed maggots.

When fully grown, the drone-fly maggot buries itself in the mud and its cuticle becomes shrunken, hard, and dark, forming the protective puparium (Fig. 105 *b*) within which the pupa is encased after the reconstruction of its parts. The puparium has the shrivelled "tail" still attached to its hinder end, but this appendage no longer serves for breathing. A pair of processes on the thorax—very small during larval life—are now standing out conspicuously ; these (*s*) are spiracular tubes communicating with the air-tube system of the enclosed pupa. On the rounded lid of the drone-fly puparium, which breaks away to allow the emergence of the fly, another pair of processes, the "anterior horns" (*c*), are visible. These have their surfaces surrounded by alternating ridges and grooves, so that they look like tiny screws ; they have no known connexion with the insect's special mode of life.

The above-mentioned examples must suffice for illustration of the various adaptations of insect larvae for life in water. From the point of view of the study of environment it is interesting to notice how such insects make use of two diverse spheres of habitation in the preparatory and perfect stages of

their lives, and since insects are pre-eminently aerial creatures, we realize from this study that the aquatic habits of the larvae must be regarded as exceptional, howsoever numerous water-dwelling larvae be. Those larvae—like the drone-fly maggot or the gnat grub—that breathe by getting contact with the atmosphere are clearly less remote from original conditions than those which—like the " blood-worm " or the immature mayfly—have the spiracles entirely closed up and are thus dependent on some respiratory organs of branchial type.

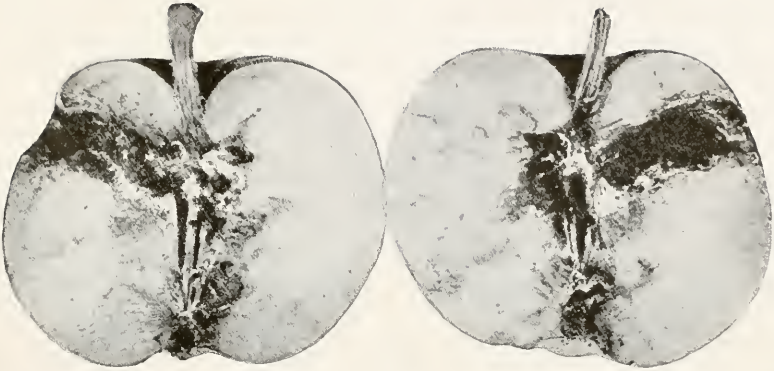
Consideration has already been given to a number of air-breathing insect-larvae of different orders that are adapted for life amid different surroundings by specially appropriate modifications of structure. It may be recalled, for example, how the caterpillars of moths and saw-flies are enabled to crawl along twigs and the edges of leaves by means of their series of paired prolegs affording support for the entire length of the body. Many caterpillars live burrowing in twigs or stems, or mining in the substance of leaves, and where the size of these larvae or the extent of the cavities in which they have to dwell, is such as to avoid any marked pressure on their bodies, there may be no marked modification of their general form. But if a caterpillar of fair size mines in a thin leaf—as that of the saw-fly *Fenusa pumilio* in raspberry canes—it may be strongly flattened from above downwards, while its prolegs become short and inconspicuous. The grubs of the wood-boring saw-flies (*Siricidae*), moving but slowly along their narrow tunnels, have no prolegs, while their thoracic legs are very short and small. Turning to the beetles whose larvae live underground, it is noteworthy how the " wireworm ", with its narrow, elongate body and hard cuticle moves rapidly through the soil, while the heavily-built chafer grubs with their relatively soft cuticle, and the pale, legless weevil grubs lie for long periods curled up in little earthen chambers. The maggot type of larva characteristic of the more highly-organized Diptera is remarkable for the great variety of conditions to which it may be fitted, for we find maggots of essentially similar structure, living in the roots of plants, mining in leaves, burrowing into vegetable refuse on cultivated land, into the masses of seaweed cast up along the tidal margin, or into animal tissues either alive or dead. The

dwelling places of insect larvae are, as might be expected, closely connected with the sources of their food supply, and this is especially evident in the case of maggots and legless grubs, creatures for the most part, of sluggish habit, which find in some organic substance, whether plant or animal, living or decaying, both shelter and food.

The varying feeding habits of insect larvae furnish a wide subject of inquiry to the student. It is during the larval stages that an insect achieves its growth in so far as increase of bulk is concerned, and among those insects which pass through complete transformations with the accompaniment of a pupal stage, a store of food material has to be accumulated to provide for the rapid growth of all the imaginal buds—both external and internal—which marks the close of the metamorphosis. In many insects, such as the whole order of the mayflies (Ephemeroptera), and certain families of Lepidoptera (*Hepialidae, Lasiocampidae, Bombycidae, Saturniidae,* for example) there is no feeding by the adult, whose only function is breeding, and all the food on which the creature is dependent for its entire life-activities must be taken by the larva. Hence it may be seen how important is this question of how or what a larva eats, and it may be understood how powerfully this factor of feeding must have affected the course of insect transformation.

A vast multitude of insect larvae feed directly on the tissues of living plants. In illustration of their variety it may be well to consider briefly the insect population of one or two common and familiar trees. On the leaves of an apple-tree[1] may be found feeding the caterpillars of many Lepidoptera—such as the bulky green larvae of the Eyed Hawk-moth (*Smerinthus ocellatus*), the restless, conspicuous hairy " tussocks " of the " Vapourer " (*Orgyia antiqua*), the brightly adorned caterpillars of the " Lackey " (*Clisiocampa neustria*), and the small dark ones of an Ermine-moth (*Hyponomeuta*) living socially on a mass of web spun by their common labour, besides the most destructive of all, the green, pale-lined " loopers " of the Winter-moth (*Cheimatobia brumata*) and its allies. These feed mostly on the foliage, but some of them also devour blossoms which furnish a particularly attractive feeding-station for some

[1] F. V. Theobald : " The Insect and other Allied Pests of Orchard, Bush, and Hothouse Fruits ". Wye, 1909.



A

B

PLATE II

A, Apples eaten by caterpillars of Codling Moth (*Carpocapsa pomonella*). B, Apples deformed through the sucking of Capsid Bugs. From *Econ. Proc. R. Dublin Soc.* II.

caterpillars, such as those of the beautiful little "Green Pug" moth (*Chloroclystis rectangulata*). During the early summer the pale pink, brown-headed "Codling" caterpillars of *Carpocapsa pomonella* are eating the tissues of the growing fruits around the cores, having emerged from eggs laid on the twigs by the mother-moth in springtime, and then eaten their way in through the "eye" of the apple (Plate II A). When fully grown the larva tunnels out through the side of the fruit and crawls along the twigs and branches and down the trunk in search of a piece of loose bark or other convenient shelter under which it may spin its cocoon. This done, the caterpillars may pass the autumn and winter in a resting condition, not undergoing pupation till the succeeding spring, or they may —in southerly districts—pupate quickly giving rise to a late brood of moths, which proceed to lay eggs on the now well-grown apples, which afford an abundant food-supply for the second (autumn) brood of caterpillars. The interior of the tree may not escape the ravages of other larvae, for the large reddish-brown caterpillars of the Goat-moth (*Cossus*) tunnel in the trunk, taking two or three years to reach their full size on the poorly nutritious diet furnished by the wood, while the little larvae of the pith-moths (*Blastodacna*) may be found in small shoots, just beneath the bark in winter, but feeding actively in the central tissue during the spring period of rapid growth. Then several tiny green caterpillars, such as that of the narrow-winged, brown *Lyonetia clerckella*, make tunnels or mines between the two skins of a leaf, eating out the soft green tissue as they pursue their winding excavations.

All the above-mentioned apple-feeding insects are caterpillars of moths (Lepidoptera); they are accompanied by many larvae of insects of other orders, which also find abundant food and shelter in various parts of the tree. Thus the legless grubs of a beetle—the Apple-blossom Weevil (*Anthonomus pomorum*) devour the hearts of the flowers, and the caterpillars of the Apple Saw-fly (*Hoplocampa testudinea*) compete with those of the Codling moth for the food-supply afforded by the fruit. Underground the large, stout grubs of the cockchafer (*Melolontha*, see p. 210) feed on the smaller roots together with the legless larvae of weevils of the genera *Phyllobius* and *Otiorrhynchus*, and it is of interest to remember that

the adult chafers and weevils will, in due time devour the shoots and leaves of the tree, the insects thus taking food from different parts of the plant at different periods of their lives.

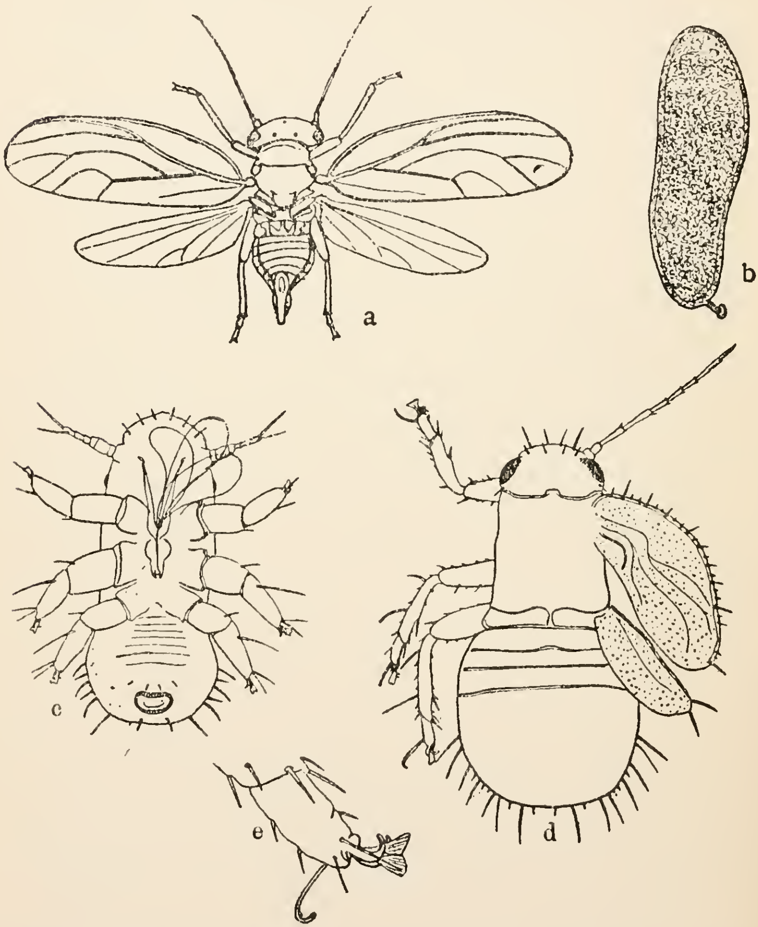



FIG. 106.
*a*, Apple-sucker (*Psylla mali*), female. × 10. *b*, egg; *c*, larva (ventral view). × 90. *d*, nymph (dorsal view, legs shown on left, feeler and wing-pads on right). × 25. *e*, foot of nymph. × 100. From Carpenter, *Econ. Proc. R. Dublin Soc.* I.

These insects—caterpillars of moths and saw-flies, larvae of beetles as well as the beetles when adult—are all provided with biting mandibles, relatively strong jaws adapted for nibbling at solid food such as pieces of leaves, petals, woody tissue,

bark, pith, fruit, or whatever it may be, particles of which are broken up and swallowed. But the apple-tree is also inhabited by hosts of sucking insects of the order Hemiptera, which, piercing the tissues with their slender needle-like mandibles and maxillae, draw supplies of sap into their stomachs. The apple-aphids (*Aphis pomi* and other species) that feed on the leaves have already been mentioned (p. 72) affording examples of insects which, in the immature stages live and feed in the same way as the adults do. In connexion with our present subject of environment, it is worthy of note that while the sucking action of one kind of aphid (*A. pomi*) may lead to a reaction of the plant tissues resulting in a curling of the leaves that tends to furnish shelter for the insects, another species (*A. avenae*) does not cause the leaves to curl in this way, and may suck from the petals as well as from the foliage. This difference goes along with a more important divergence in habit, for while *A. pomi* remains on apple throughout the summer—its winged females leaving their native shoots simply to fly to other apple trees—*A. avenae* is a migratory aphid, its winged virgin females leaving the apple altogether in spring and going off to spend the summer in the ears of oats. Within the blossom-buds in spring may be feeding the curious tiny larvae and nymphs of the sucker (*Psylla mali*, Fig. 106, *c d*), differing strongly in appearance as well as in behaviour from the adult Psyllae (Fig. 106 *a*) which fly and jump actively about the shoots later in the year. The eggs (Fig. 106 *b*) of these insects, with short stalks and bright yellow in colour, are attached to the bark of the twigs; and the newly-hatched larvae which come out of them crawl along to the unopened buds, on which they wait till the young leaves begin to expand and the shoots to lengthen, affording the insects the opportunity of entering the developing blossoms. On the bark of the branches may be found crowded together the passive females of the Mussel-scale (*Mytilaspis pomorum*, Fig. 49) each fixed to the tree by her very long and flexible piercers, and covered by the protective scale, which serves also a shelter for the winter eggs; the larval scale-insects (Fig 48, p. 89) move about over the bark in spring time, till they assume the nymphal condition and settle down for the resting period of the life-history. In crevices of the bark may also be found

communities of the Woolly Aphid (*Schizoneura lanigera*) with their white, waxy, cotton-like, protective covering—virgin females and their young in various stages of growth all living in the same way; further societies of the woolly aphid may be found also on the woody roots. The presence of these sucking insects on the branches and roots results in a response of the plant tissues giving rise to swellings, distortions, and abnormal growths.

Ripe apples are occasionally to be found the skin of which is cracked, deformed and partly peeled off (Plate II B). This condition is due to the presence on the fruits, during the time of growth, of immature capsid plant bugs [1]; their puncture of the soft, developing tissues for feeding with the accompanying injection of saliva causes decay of the adjacent part of the plant. This mode of feeding on apples by capsid bugs in their early stages is a new phase of behaviour on the part of these insects. One of the species (*Plesiocoris rugicollis*) is known to have used willow-foliage, as the usual source of its food supply, and there is no doubt that in various localities migran of this species are leaving willow to feed on apple, giving thus a remarkable illustration of the tendency often shown by living creatures to change their surroundings, and to adopt new habits of life.

It is of interest to notice how the larvae of some insects appear to be dependent for their food supply entirely on some one kind of plant, while other larvae are able to feed equally well on a great variety of plants. For example the caterpillars of the Winter and Vapourer moths, mentioned above, as common pests of apple, may be found on the leaves of an extensive series of deciduous trees, showing great power of adaptability to different surroundings as regards food. Other larvae are able to avail themselves of a wide choice of food-plants within the limits of one large order; for example, some of the small ermine (*Hyponomeuta*) caterpillars that feed on apple will live and thrive on other rosaceous trees, such as hawthorn, and hawthorn was probably the original rosaceous food-tree of the Woolly Aphid (*Schizoneura*) in North America, its native country. On the other hand caterpillars of such specialized

[1] J. C. F. Fryer: "Capsid Bugs". *Journ. B. Agri.*, Vol. XXII., 1916. K. M. Smith: "Damage to Plant Tissue from the Feeding of Capsid Bugs." *Ann. Appl. Biol.* VII., 1920.

feeding habits as the leaf-miner *Lyonetia clerckella* and the Codling (*Carpocapsa pomonella*) are usually confined to the apple, though the latter may be observed, on occasion, feeding in growing pears and plums also. As an example of a very common insect with closely restricted feeding habit the Small Tortoiseshell butterfly (*Vanessa urticae*) may be mentioned; its spiny caterpillars are to be seen only on stinging-nettles, and the same is the case with its ally the Peacock butterfly (*Vanessa io*).

Reference has been made to willows as the original home and food-supply of some of the capsid bugs that suck sap from growing apples. The willows—including the various forms of osiers and sallows—harbour an assemblage of insect larvae as interesting as those found in apple orchards, and illustrating some further features of life-relations. The big caterpillars of the Eyed Hawk-moth (*Smerinthus ocellatus*) feed on willow leaves as readily as on apple foliage, while the small, active larvae of a gelechiid moth (*Depressaria conterminella*) may be found at the ends of osier shoots in late spring, having provided for themselves a shelter by rolling the narrow, elongate leaves and fastening them together by means of their silken threads. Passing over a large assemblage of moth-caterpillars that feed on the leaves of willows, as well as on those of other deciduous trees, special mention may be made of the feeding habits of the larvae of the beautiful yellow "Sallow" moths (*Xanthia flavago* and *X. fulvago*). Emerging from the eggs, which, laid in autumn by female moths, are the wintering stage of these species, the caterpillars begin in spring to feed on the catkins of sallows (*Salix caprea*), wherewith their pinkish mottled coloration harmonizes well. Before they attain their full growth the catkins may be withered, in which case the larvae transfer themselves to plantain or bramble leaves.

Besides caterpillars of many moths, those of several species of saw-fly also feed on willows. The social larvae of *Pteronus salicis*, for example, of which there are early summer and late autumn broods, eat the foliage voraciously, so that only the veins of the leaves escape destruction. But the willow-feeding saw-fly larvae furnish interesting examples of that mutual reaction between an insect and the plant on which it lives, that results in the formation of a *gall*. Beneath willow-leaves

in summer and early autumn may often be seen small spherical bodies like succulent fruits, greenish yellow in colour, with red markings; these are galls of *Pontania salicis*, and each contains a chamber within which the larva finds protection and nourishment. In correspondence with its concealed dwelling-place this larva is pale in colour; it feeds on the modified plant tissue of which the gall is built, and when fully fed, it descends to the soil for pupation. Next spring the flies—black and yellow insects with clear wings—emerge from the buried cocoons and lay their eggs in incisions, cut with their serrate ovipositors below the leaves. The plant-tissues are irritated by this action, or by the pressure of the egg, so that they respond by developing the characteristic and regular gall, which comes to surround the eggs; thus the larva when hatched finds itself provided with abundant food and effective shelter. Other saw-flies of the same genus (*Pontania*) have larvae that live in galls on the leaves and shoots of willows.

The gall-forming habit is a highly interesting subject of study in connexion with the life-relations of insect-larvae.[1] A gall may be regarded as a pathological growth, a diseased excrescence due to the presence of the egg or the larva in the plant-tissues; but, by producing a gall, the plant provides food for the insect at less expense to itself than by letting the insect devour indiscriminately its leaves and shoots. Only a comparatively few saw-fly caterpillars are gall-feeders, but the great majority of larvae of another hymenopterous family, the *Cynipidae* or Gall-flies, distinctively live in this manner; and the oak is the tree that harbours the greatest variety of them. The familiar "oak-apples", the fruit-like "cherry-galls" below the leaves, the beautiful "spangles" or button-galls, the curious cottony growths on the shoots are all due to the presence of various cynipid larvae. Although the female gall-fly has a long piercing ovipositor by means of which she inserts her eggs into the tissues, it is apparently neither the irritation due to the act of egg-laying nor the presence of the egg, but a secretion of the larva after hatching which serves as the stimulus leading to the responsive gall-forming growth on the part of the plant. It is remarkable that the larvae of

[1] C. Houard: Les Zoocécidies des Plantes d'Europe et du Bassin de la Méditerranée". Paris, 1908-13. E. T. Connold: "Plant-galls of Great Britain". London, 1909.

nearly-related species of gall-fly, and even those of alternate generations of the same species produce galls of widely different appearance and texture.[1] The "cherry-galls" of *Dryophanta*, for example, beneath oak leaves, are inhabited by larvae hatched from fertilized eggs laid by females in the leaves about midsummer. These larvae pupate within the galls, whence emerge in midwinter—when the galls are no longer succulent, but dry and hard—larger virgin females which lay eggs in the buds of the tree. The buds are arrested in their growth and form small violet galls, visible on the branches in springtime, from which the summer sexual brood of flies emerge to lay their eggs in the leaves, whereon the cherry-galls are produced as a reaction to the presence of the larvae. The gall-flies are all of small size, and the larva, a legless grub with small head and soft cuticle, like the great majority of hymenopterous larvae, lives passively within the chamber of the gall, its body bent so as to fit the sub-spherical cavity.

From cynipid galls there frequently emerge insects not of the gall-producer's species, though of the same family. These are inquilines or "cuckoo-parasites", the female fly having laid her eggs in a gall already formed in response to the irritation set up by its proper larva. From this egg is hatched the inquiline larva which feeds on the gall-tissues rightly belonging to the latter. A few cynipid larvae live as parasites; hatched from eggs inserted into a gall, they devour its rightful occupier, and then, completing their transformations, appear as an unexpected type of fly.

Returning now to the willows, we may find several examples of galls due to the presence of insects of another order—the *Cecidomyidæ* or gall-midges, a family of the Diptera. In summer it may be seen that some of the buds on willows and osiers have been arrested in their growth; instead of lengthening to form normal shoots, they become changed into spreading rosettes of small reduced leaves which are covered by a dense hairy coating. Within the shelter afforded by this simple type of gall, the little yellow larvae of a gall-midge, *Rhabdophaga heterobia*, may be found living six or eight together. These grubs (Fig. 107 *b c*) have a very small head, a series of

[1] H. Adler and C. R. Straton: "Alternating Generations". Oxford, 1894.

paired spiracles along the body-segments and on the ventral aspect of the prothorax a characteristic sternal process or "breastbone" (*d*), a little anchor-shaped sclerite, which differs in its exact form in the various species. The larvae remain in the galled buds through the winter and pupate there,

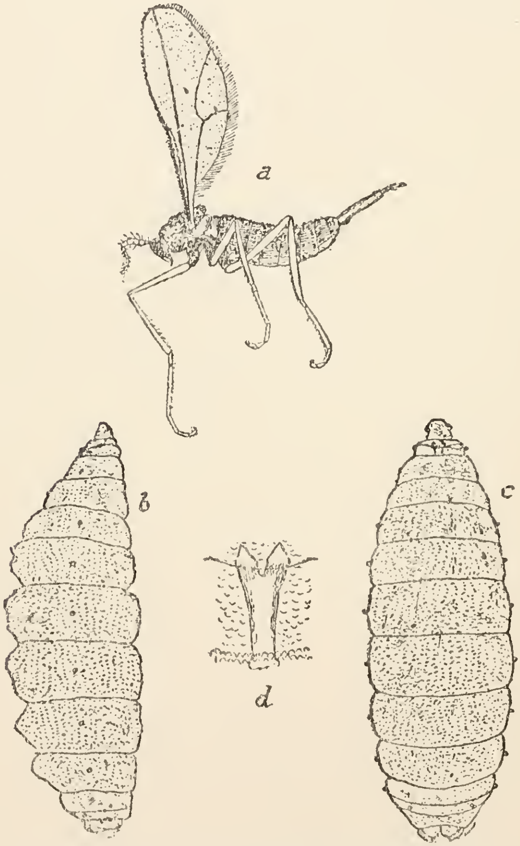



FIG. 107. WILLOW GALL-MIDGE (*Rhabdophaga heterobia*).
*a*, female (side view); *b*, larva (side view); *c*, larva (ventral view). × 50. *d*, anchor-process of larva. × 150. From Carpenter, *Econ. Proc. Dublin Soc.* I.

the little, hairy, black midges emerging in the ensuing year. The gall-midges may be recognized by the very simple nervuration of the wing; the female (Fig. 107 *a*), as is the case in many other Diptera, has the hinder segments of the abdomen protrusible, so as to form an elongate "ovipositor", but this has no


PLATE III.

Osier Shoot, showing work of Gall Midge (*Rhabdophaga saliciperda*). In J, the bark is peeling off. In K, the bark and outer wood have been removed to show the larval chambers. In L, the bark shows numerous exit holes through some of which pupal cuticles are protruding. From *Econ. Proc. R. Dublin Soc.* II.

cutting organs for making incisions in plant tissues ; it is simply inserted between the leaves of the bud, so as to deposit the eggs where the young larvae will—owing to the plant's response to their presence—find effective shelter and abundant food.

Several other kinds of gall-midge[1] inhabit willows during their larval period. The female of *Rhabdophaga saliciperda*, for example, lays her eggs on the bark in June and July, and the larvae eat their way into the wood, where their presence stimulates the growing tissue to produce irregular swellings wherein they find shelter and food through the autumn and winter, each yellow grub occupying a little oval chamber. In the succeeding spring they pupate beneath the bark, and the pupae work their way partly out of the shoots through small round holes in the bark, from which the delicate white pupal cuticles may be seen protruding after the emergence of the midges in spring and early summer (Plate III). The activities of these insects may render the trees which they inhabit unsightly, as the bark is ruptured so that it hangs down in shreds on account of the abnormal growth of the underlying woody tissue. In the case of these dipterous gall-midges, the correlation between plant and insect is less complete and harmonious than in the case of the hymenopterous gall-flies of which examples have been given in connexion with oak-trees, or the gall-forming saw-flies mentioned above as characteristic insects of the willow itself.

In summertime the leaves of willows and osiers are often so severely eaten as to appear riddled and torn into multitudinous holes. This is the work of the willow-leaf beetles (*Phyllodecta*) (see p. 110, Fig. 61) and their larvae. The small, metallic, dark-hued beetles come out of winter quarters beneath loose pieces of bark, the eaves of sheds and such shelters, and lay their eggs on the leaves. The well-armoured larvae live like their parent beetles, feeding openly on the willow-leaves. The beetles, more than any other order of metamorphic insects, afford examples of imago and larva, living and feeding in the same manner, and this is in some cases correlated with loss of power of flight on the part of the beetles. An extreme instance of this tendency is afforded by the female of Lampyris,

[1] J. J. Kieffer : " Monographie des Cecidomyides d'Europe et d'Algérie ". *Ann. Soc. Entom. France*, LXIX. 1900.

the "glow-worm", which is not only wingless, but resembles closely in outward aspect the woodlouse-like larva characteristic of her family.

Most of the vegetable-eating beetles, however, display—as is usual in metamorphic insects—a larval method of feeding diverse from that of the imago. Reference has already been made (p. 110, Fig. 62) to the chafer grubs which live underground and feed on roots while the adult beetles devour leaves, and (p. 112, Fig. 63) to the caterpillar-like grubs of leaf-beetles of the "turnip-fly" group which mine in leaves or burrow in the interior of stems of herbaceous plants. Such larvae feeding in these concealed situations have a soft, flexible cuticle over the body-segments with small and feeble bristle-bearing

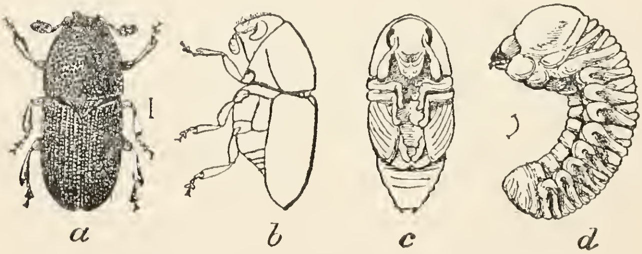



FIG. 108. BARK-BEETLE (*Scolytus rugulosus*).
*a*, dorsal view; *b*, side view; *c*, pupa (ventral view); *d*, larva (side view). × 20. From Chittenden, *U.S. Dept. Agric. Entom. Circ.* 29.

tubercles. The white, legless, fleshy grubs of weevils (p. 114) are all concealed feeders, living underground and eating roots like the larvae of the Vine-weevils (*Otiorrhynchus*), mining in leaves like the Beech-weevil grub (*Orchestes fagi*) whose presence between the leaf-skins gives rise to conspicuous brown blisters, or boring in wood like the larvae of *Hylobius abietis*, the large Pine-weevil. The whole family of the bark-beetles (*Scolytidae*)[1] have legless grubs (Fig. 108 *d*), with white, wrinkled cuticle, like those of weevils. Boring through the bark of the appropriate food-tree, the female beetle (Fig. 108 *a b*) eats out a tunnel on the inner aspect of the bark laying eggs along it on either side at regular intervals. The larvae, when hatched, burrow along lateral tunnels opening out from the mother-

[1] W. Eichhoff: "Die europäischen Borkenkäfer". Berlin, 1881. A. T. Gillanders: "Forest Entomology". Edinburgh, 1908.

PLATE IV.

Galleries of large Ash Bark-beetle (*Hylesinus crenatus*) in old ash trunk. From A. C. Forbes, *Irish Nat.* XIX.

gallery ; these tunnels increase in diameter as the larvae grow larger, and terminate in oval chambers wherein they pupate (Plate IV). Each young beetle after its emergence from the pupal cuticle bores its way straight out through the bark, which viewed from outside looks as if pierced by numerous small shot-holes.

Besides the large number of insect larvae that feed on living plant-tissues, of which a small selection has been mentioned in the preceding pages, very many live on dead or decaying vegetable matter, playing thus the part of scavengers in the economy of nature. In a rotten potato or turnip, for example, there may often be found a crowd of narrow, elongate, whitish grubs with small heads, feeding greedily on the decaying mass. These come from the eggs of *Mycetophilidae* or fungus-midges, a family of Diptera related to the *Cecidomyidae* or gall-midges mentioned above. The Diptera are noteworthy among insects for the number of their species whose larvae act as scavengers, and this habit is especially characteristic of the maggot type of larva. The common house-fly (*Musca domestica*)[1] furnishes the best-known example of this relationship. The flies often lay their elongate, white eggs in heaps of decaying vegetable refuse, such as the contents of garden bins, and into this the maggots, when hatched, work their way. A condition of fermentation in the material is especially attractive to the flies about to lay their eggs, and a rise in temperature always hastens the development of the maggots, so that the larval stage may last only a week. House-fly maggots will also feed in dry dustbin refuse, such as papers and rags, or in the remains of old mattresses, but the substance which more than any other serves them for food is horse-dung, which may be defined as animal excrement consisting largely of vegetable remains, because of the grazing and grain-eating habits of the horse. Manure-heaps form, therefore, highly attractive breeding-places for flies. They also seek exposed human excrement for the purposes of egg-laying, and in this way they readily become carriers of disease-germs into human dwellings and on to human food. The familiar house-fly affords an example of an insect in which the surroundings of the imago often differ strikingly from

[1] C. Gordon Hewitt : " The House-fly ". Cambridge, 1914.

those of the larva, and herein lies its danger to man, its unwilling host. A house in which house-flies could find suitable breeding material would be an exceptionally dirty place, but these insects often come straight from the unspeakable filth in which they lay their eggs, to walk over butter or fall into uncovered milk-jugs. Thus typhoid and infantile diarrhoea are spread, and it is realized how important for the health and welfare of human societies may be a knowledge of the surroundings amid which common insects and their larvae live.

While decaying plant-tissues, refuse and excrement furnish thus a rich food supply for diverse insect larvæ, many others live in the bodies of dead animals. In the *Silphidae* or carrion-beetles, we see a family of insects in which the carrion-feeding habit is prevalent both among adults and larvae. The well-armoured woodlouse-like grubs of species of *Silpha* (Fig. 58) wander about in search of dead animals on which they may feed, though some of them seek other sources of nourishment, such as live snails which they hunt and devour. The well-known burying-beetles (*Necrophorus*) work in companies, interring the bodies of small beasts and birds, on which they lay their eggs so that the larvae, when hatched, find themselves close to a large mass of suitable food. In correspondence with their quiescent mode of life these Necrophorus grubs differ from the armoured Silpha larvae, having a softer cuticle beset with spiny plates. Turning to the Diptera, it may be noticed that some of the most abundant and familiar of insects, such as the blue-bottles (*Calliphora*) the green-bottles (*Lucilia*), and the large, grey flesh-fly (*Sarcophaga*), lay their eggs (the notorious " fly-blow ") on flesh, into which the maggots, with their strong, sharp mouth-hooks, quickly eat their way. On this highly nutritious food they grow fast, and pass rapidly through the successive stages of the life-history, so that the flies of a second generation may appear in a fortnight.

Many cases are on record of blue-bottle maggots feeding on or in the bodies of living animals instead of in dead flesh. This horrible habit on the part of the larvae is a sequence to the act of the female fly in laying her eggs on a live instead of a dead animal, and it has been observed that neglected sores or wounds prove especially attractive to the flies, which on occasion make use of human beings for egg-laying. In

these countries and other parts of Western Europe, a species of green-bottle (*Lucilia sericata*), is so notorious for its habit of laying eggs on the wool of live sheep, that it has become known as the "Sheep-maggot Fly". The maggots (Fig. 75) when hatched begin to bite their way into the skin of the sheep; if present in large numbers, and unchecked, they may burrow deeply into the muscular and fatty tissue, causing, finally, the animal's death. Years ago the attacks by this fly on sheep were said to have been confined to low-lying, rich pastures, but now flocks on mountainous highland grazings are frequently troubled.[1] The area in which the habit prevails is therefore extending, and it is of interest in this connexion to notice that since the introduction of immense flocks of sheep into the inland districts of Australia, several species of muscoid flies, native to that continent, have taken to the same method of egg-laying.[2] Such behaviour on the part of these insects, repulsive though it be, is of much interest to the naturalist because it affords examples of a widespread change of habit in a species or group of species, whose members are abandoning the scavenging method of larval feeding, and are taking instead to a parasitic life in the bodies of large animals. And it is highly instructive to recognize that this change of habit follows as the result of a marked change in the surroundings of the insects in certain parts of their geographical range. Great flocks of sheep form, for example, a new element in the environment of insects native to Australia.

The recently acquired parasitic habit of these sheep-maggots is clumsy and disharmonious, leading to great suffering and frequently to death on the part of its host. There are, however, many kinds of flies whose larvae live in the bodies of large animals in such a manner that the parasitism is specialized; these cause the host comparatively slight inconvenience unless they be present in abnormally large numbers. Naturally the life-histories of those parasitic on domesticated animals have been especially studied, and it is well to remember that domestication, involving the comparative crowding of many beasts of the same kind on a restricted area, tends to

[1] R. S. MacDougall: "Sheep-Maggot and Related Flies". *Trans. Highl. Agric. Soc.* 1909.

[2] W. W. Froggatt: "Sheep-Maggot Flies". *Bull. Dept., Agri., N.S. Wales.* 1915–18.

increase largely the risk of infection and the numbers of the parasites. The sheep harbours the larvae of one of these specialized parasitic flies (*Oestrus ovis*), a greyish, heavily-built insect with vestigial mouth-parts so that it takes no food in the adult state. The female Oestrus lays eggs, or deposits active maggots which have hatched within her body, in the sheep's nostrils, whence the maggots make their way into the nasal air passages, and subsequently into the frontal sinuses of the head where they become fully grown. Being finally coughed out by the sheep, they pupate on the ground in preparation for the flies of the next generation.

An excellent example of specialized parasitism is afforded by the Ox Warble-flies (*Hypoderma*), usually grouped in the same family[1] as Oestrus, which they resemble in their reduced jaws and abstinence from feeding in the winged condition. They are hairy flies, coloured like bumble-bees, and flying in the summer sunshine with a distinct hum. The " fly season " for our two native species of Hypoderma (*H. bovis* and *H. lineatum*) lasts from May till September. The female fly (Fig. 109 *a*) pursues cattle grazing in the fields, and lays her curiously-shaped eggs (Fig. 109 *c*), each with a grooved base, astride the beast's hair usually low down on the legs. The larva of Hypoderma is a muscoid maggot, modified for its special mode of life, and passing through somewhat marked changes of form in the course of its life-history in correlation with its migrations through the host's body. The first-stage maggot (less than a millimetre long) is elongate and very spiny, with powerful divergent mouth-hooks between which is a strong median spine formed of paired sclerites (Fig. 109 *f*). This formidable armature is used by the maggot first for breaking its way out of the egg-shell, and then, for boring into the skin of its host ;[2] the little larva crawls along the hair and uses the hair-follicle as a starting-point for its tunnelling operations.[3] Working along beneath the skin, the maggots migrate to the gullet of the host, for they may be found in

[1] Bracy Clark : " An Essay on the Bots of Horses and other Animals ". London, 1815. F. Brauer : " Monographie der Oestriden ". Wien, 1863.

[2] G. H. Carpenter and T.R. Hewitt : " Some new Observations on the Life-history of Warble-flies ". *Irish Nat.*, XXIII. 1914. And *Journ. Dept. Agric., Ireland*, XV. 1914.

[3] S. Hadwen : " Contribution to the Biology of Hypoderma lineatum ". *Bull 21 Health of Animals Branch, Canad. Dept. Agric.* 1916.

numbers from August until January in the gullets of slaughtered cattle, embedded in the sub-mucous coat. They are now in the second stage (from 5 to 12 mm. long),[1] with the spiny armature on the segments hardly perceptible, except for a few short black spines near the tail-spiracles (Fig. 109 *e*). From December onwards they begin to appear, still in the

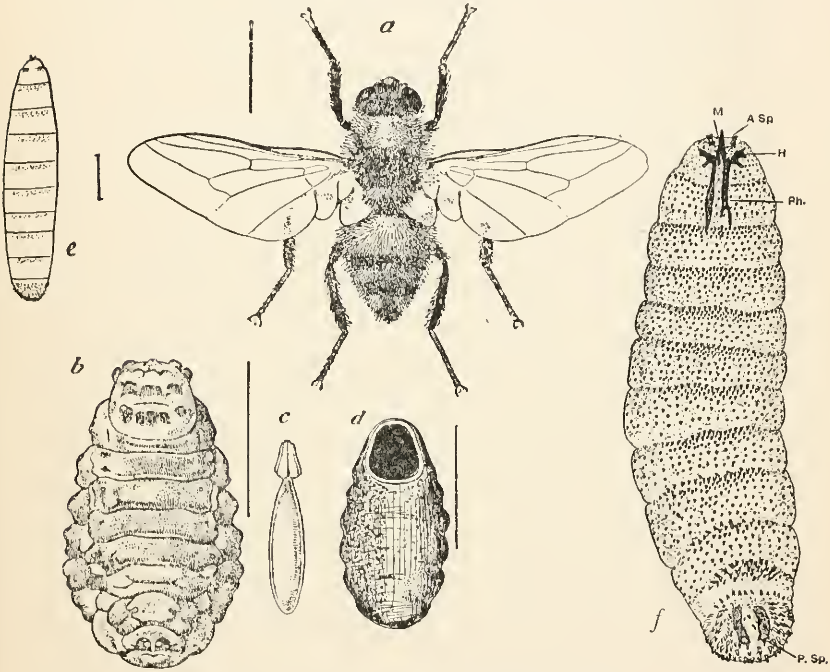



FIG. 109. OX WARBLE-FLY (*Hypoderma bovis*).

*a*, female. × 2½. *b*, full-grown (fourth stage) larva (dorsal view). × 2. *c*, egg. × 20. *d*, empty puparium (lid broken away). × 1½. *e*, second stage maggot (from gullet of cattle). × 5. *f*, first stage maggot (*H*, mouth-hooks; *M*, median spine; *Ph*, pharyngeal sclerites; *A. Sp*, anterior, and *P. Sp*, posterior spiracles). × 70. *a*—*d*, from Theobald, "Report on Econ. Zool". I; *f*, after Carpenter and Hewitt, *Proc. R. Dublin Soc.* XIV.

second stage, beneath the skin of the back, having migrated by way of the diaphragm, or the neck and back-muscles, and the vertebral canal. The mouth-armature of the second stage larva is fairly strong, and is doubtless serviceable in biting a passage through the tissues. Soon after arriving beneath the skin of the back, the maggot assumes its third condition; there are now distinct rows of spines on the ventral

[1] E. W. Laake (*Journ. Agric. Res.* XXI No. 7, 1921) states that two distinct instars are included in this "second stage."

aspect of most of the segments, but the mouth-armature has become extremely feeble, the hooks being far smaller than those in the first or second stage. The larva, relatively stouter than in the previous stages, has now no further paths to travel through the tissues, but it makes a hole through the skin and lies with its tail-spiracles just beneath this hole, and therefore in touch with the atmosphere, while its body, directed obliquely downwards, lies in a cavity—the hollow of the small tumour or "warble" due to its presence. This swelling increases with the growth of the maggot, which, after another moult, enters its fourth and final stage (Fig. 109 *b*). Its spiny armature is now again strong; as in the first stage there are dorsal as well as ventral rows of spines on most of the body segments, and the tail-spiracles are large and conspicuous, but the mouth-hooks are minute. During the third and fourth stages the maggots feed by imbibing the fluid which exudes from the inflamed tissues affected by their presence. Ripe warbles, forming prominent swellings along the host-animal's back on either side of the spine, are evident from February on till May or June, and the fully fed larvae become barrel-shaped and dark in colour. Ultimately each maggot works its way through the breathing-hole in its host's skin and falls to the ground, where it pupates, the hardened larval cuticle forming a firm, black puparium (Fig. 109 *d*) from the front end of which a round lid splits off to allow the escape of the fly. The pupal period lasts about six weeks.

While many insect-larvae live thus as parasites in the bodies of large animals, a far greater number are parasitic in other insects, the female adult laying her eggs on the body of an appropriate host, or if, as is usually the case, she possesses a piercing ovipositor, inserting this through the cuticle and skin so that the eggs are laid among the internal tissues on which the larvae feed. The vast majority of these insect-larvae parasitic in other insects, feed on the larva of their host, and a single species of insect may serve as host to a large company of parasites. For example, caterpillars of the Gipsy moth (*Porthetria dispar*), a common European species, often destructive in woodlands, and inadvertently introduced some years ago into the eastern United States, are known to serve as hosts for more than forty hymenopterous and twenty-six

dipterous parasites.[1] Many of these can feed indifferently on a number of hosts.

The Diptera, whose larvae live in this manner, are mostly members of the family *Tachinidae*, allied closely to the blue-bottle family (*Muscidae*), but with the adults distinguished by the absence of fine hairs (" feathering ") on the terminal " bristle " of the feeler. Most tachinid flies—*Tachina larvarum* (Fig. 110), for example—deposit their eggs on the body of the host-caterpillar, into which the maggots, when hatched, bore

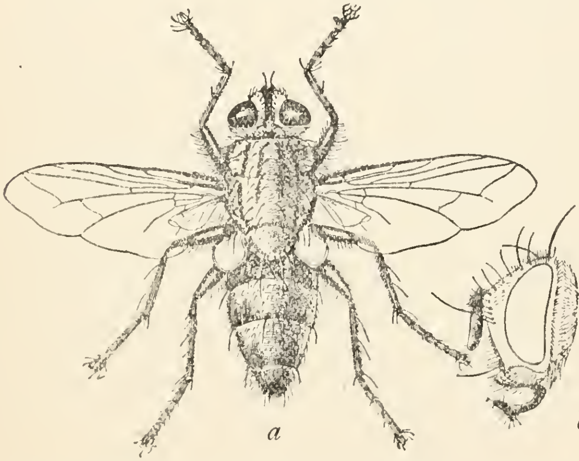



FIG. 110.
*a*, *Tachina larvarum*, a Parasitic Muscoid (female). × 5. *b*, head of *Tachina* (side view) showing eye, proboscis, and feeler with unfeathered bristle. × 10. From Howard and Fiske, *U.S. Dept. Agric. Ent. Bull*, 91.

their way by means of their sharp mouth-hooks ; the maggot of Tachina devours the moth-caterpillar internally, and generally kills it before the pupa has been formed. *Compsilura concinnata*, another tachinid, is " viviparous ", the eggs hatching within the vagina of the mother, whose sharp " larvipositor ", situated beneath the abdomen, pierces the caterpillar's skin and thus places the tiny maggot safely inside the host's body ; the maggots make their way to the wall of the food-canal in which they feed. Most remarkable is the habit of *Blepharipa scutellata*, whose eggs are laid

[1] L. O. Howard and W. F. Fiske : " The Importation into the United States of the Parasites of the Gipsy Moth and the Brown-tail Moth ". *U.S. Dept. Agri. Entom. Bull. No.* 91. 1912.

haphazard on leaves of trees where the host caterpillars are feeding (Fig. 111 *a*), so that these may swallow them as they eat the leaves. The Blepharipa maggots (Fig. 111 *b*) eat through the

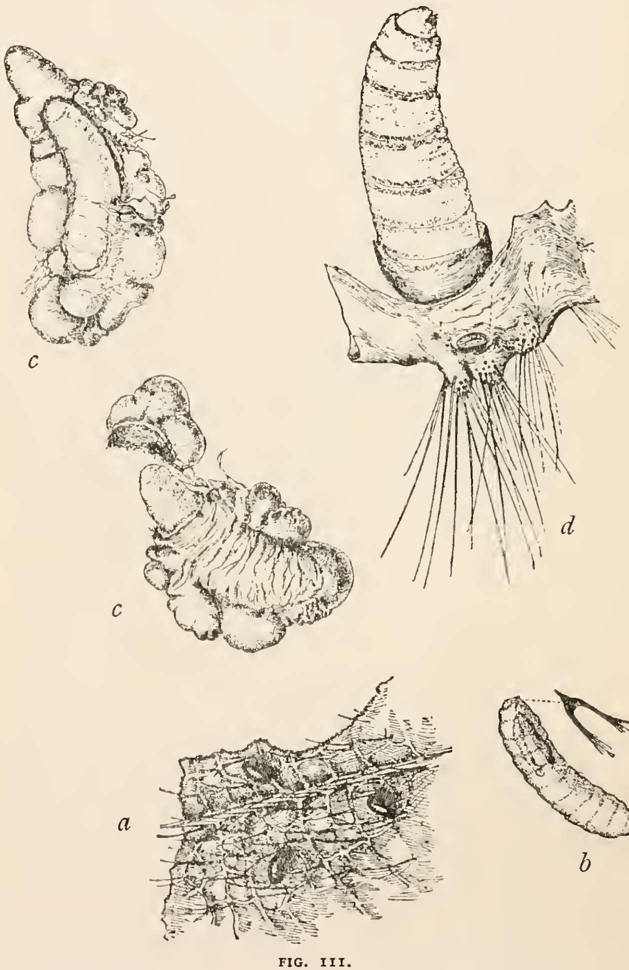



FIG. 111.

*a*, Eggs of Tachinid-Fly (*Blepharia scutellata*) on leaf. × 5. *b*, first stage larva with mouth-hooks ; *c*, *c*, first stage larvae in modified tissues of their host-caterpillar ; *d*, second stage larva with its tail-end in tracheal "funnel" of host close to spiracle. ×25. From Howard and Fiske.

wall of the food-canal in which they are hatched, and embed themselves in the caterpillar's tissues which appear to undergo an abnormal gall-like growth (Fig. 111 *c*) as the result of their presence. After a moult they are found in enlarged and

modified tracheal tubes with their tail-spiracles just within the opening of one of the caterpillar's spiracles (Fig. 111 *d*). This parasite usually allows its host to pupate; then it

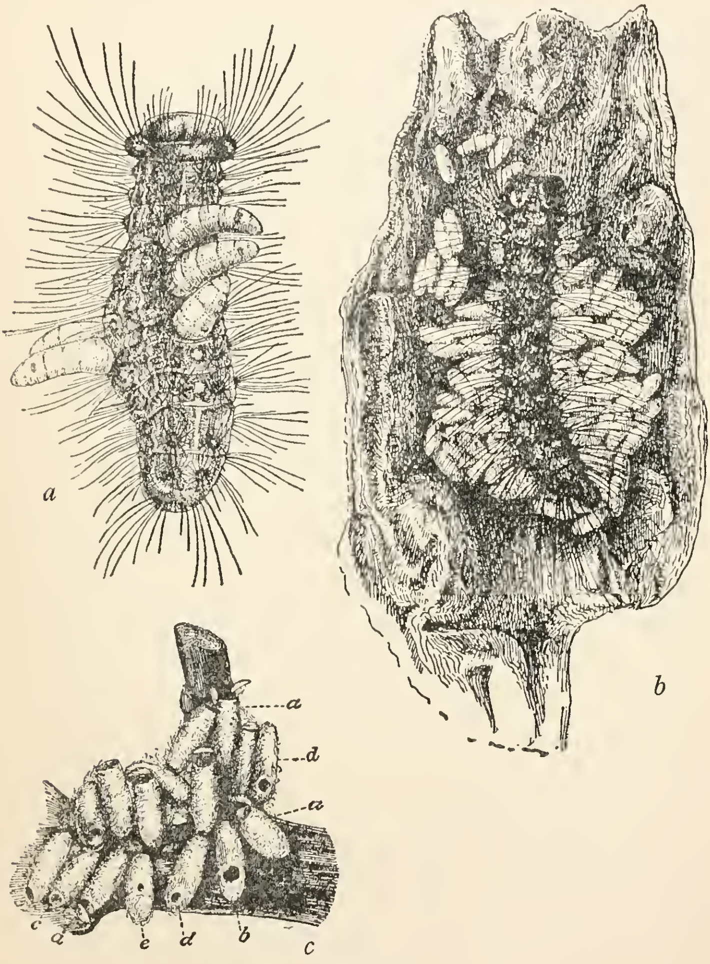



FIG. 112.
*a*, Larvae of Ichneumonoid (*Apanteles fulvipes*) eating "Gipsy" caterpillar. × 1½. *b*, cocoons of *Apanteles* surrounding dead caterpillar, slightly enlarged. *c*, cocoons from which *Apantele.* (*a*) and its various secondary parasites (*b*, *c*, *d*, *e*) have emerged. × 2. From Howard and Fiske.

devours the pupa internally, becomes full-grown, and itself pupates in the soil.

Of the hymenopterous parasites of insect-larvae, the most

conspicuous are the Ichneumonoidea—slender, wasp-like insects of which there are several families (*Ichneumonidae, Braconidae,* etc.). All have formidable ovipositors, by means of which they pierce the cuticle and skin of the host, and thus place their eggs inside the body. Some, such as *Rhyssa* with ovipositors of enormous length can bore through the bark and wood of trees and thus reach the tunnels of the timber-eating larvae in which their grubs feed. Large ichneumons, like *Ophion* and *Pimpla,* lay one egg in each caterpillar they attack ; the ichneumon larva may eat its way out of the host before the latter has become full-fed, and spin on the food-plant or on the ground the cocoon in which its pupal stage is passed ; or it may not emerge from the host-caterpillar until this has spun its own cocoon, the last act it is able to perform before dying, a victim to its parasite which then, emerging from the shrivelled cuticle, spins its own cocoon inside the host's, so that the emerging ichneumon-fly has two cocoon walls to pierce before emergence. Small ichneumonoids—such as species of the Braconid genus *Apanteles*—lay many eggs in one good-sized caterpillar, the dried cuticle of which may be seen pierced by the holes through which the little parasitic grubs emerge (Fig. 112 *a*) and surrounded by the silken cocoons, in which they pupate after emergence (Fig. 112 *b*). All these ichneumonoid grubs are legless and with small heads, like those of bees and wasps (p. 126), and the great majority of hymenopterous larvae.

Some of these hymenopterous parasites are noteworthy as affording examples of different forms succeeding each other in the same life-history (hypermetamorphosis, p. 116). Species of *Platygaster* lay their eggs in some of the larvae of midges mentioned above as living in galls on willow (p. 211). The newly-hatched larva of Platygaster[1] (Fig. 113 A) is remarkably like a little copepod crustacean, having a large, oval front-region comprising the head and thorax, with short feelers and biting mandibles, and a narrow abdomen with a reduced number of segments. This is succeeded by a second stage (Fig. 113 B), in which the body is elliptical in outline, not differentiated into regions, and with the segmentation generally undefined. Not until its third stage does the Platygaster larva assume the form

[1] J. Ganin : " Beiträge zur Kenntniss der Entwiklungsgeschichte bei den Insekten ". *Zeisch. f. wissensch. Zoolog.*, XIX. 1869.

of the soft-cuticled, small-headed grub characteristic of its group (Fig. 113 C).

The study of insect-larvae parasitic in other insects is complicated by the fact that frequently the parasite itself is attacked by a "secondary" parasite, and this in some cases by a "tertiary" parasite. Such "hyperparasitism" is illustrated in some of the tachinids and ichneumonoids that live on the "Gipsy" caterpillars mentioned above. An exceedingly small chalcid (*Melittobia acasta*), of which the male is

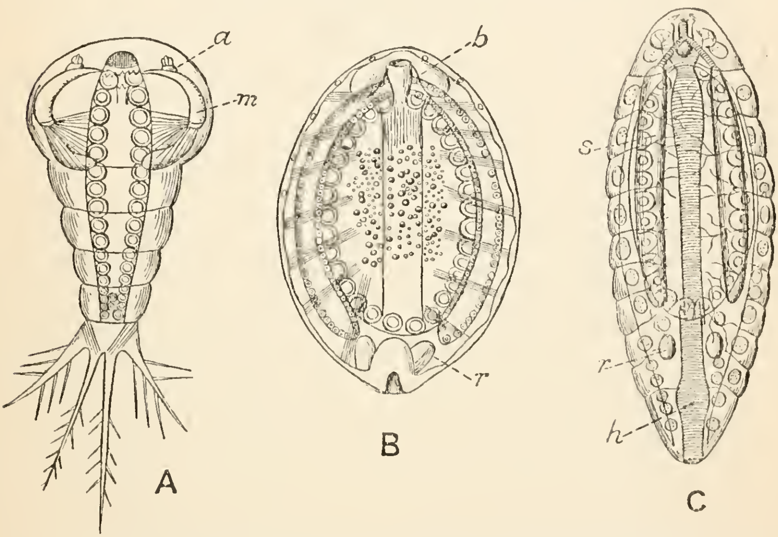



FIG. 113. THREE LARVAL STAGES OF PROCTOTRUPID PARASITE (*Platygaster*).
*A*, First stage ("cyclops") larva (*a*, feeler; *m*, mandible). × 160. *B*, Second instar (*b*, brain; *r*, ovary); *C*, Third instar (*h*, intestine; *s*, salivary gland; *r*, ovary). × 80. After Ganin, *Zeitsch. f. wissensch. Zool.* XIX.

blind and wingless, is a most deadly enemy of the tachinid Blepharipa, in the buried puparia of which the active little females, possessed of remarkable faculties for discovering their victims and able to penetrate through the narrowest crevices, lay their eggs. From a very large percentage of the cocoons of Apanteles emerge not that insect, but various hyperparasites, whose larvae have fed on the Apanteles pupae. The presence of these intruders is recognized by the round holes (Fig. 112 *b c d*) which they bore in emerging through the side of the cocoon, whereas the Apanteles imago comes out by the lifting of a neat circular cap at one end (Fig. 112 *a*).

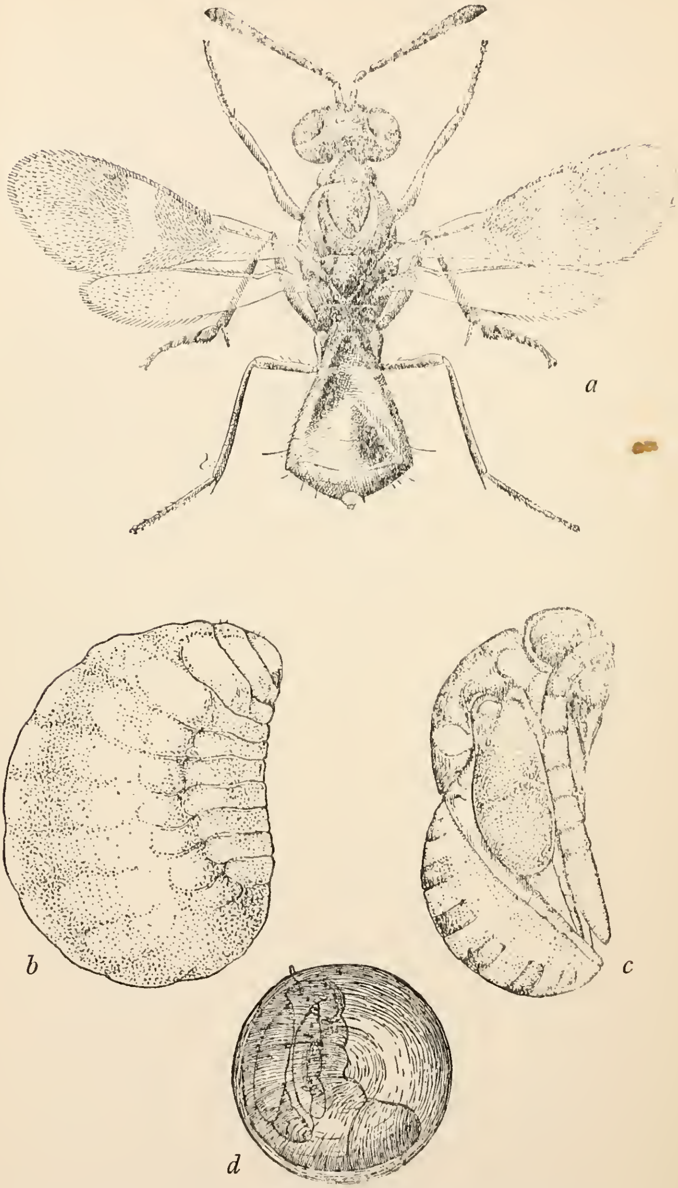



FIG. 114. EGG-PARASITE (*Anastatus bifasciatus*) OF GIPSY-MOTH.

*a*, female; *b*, larva; *c*, pupa. × 60. *d*, egg of gipsy-moth parasitized by larva of *Anastatus* within which larvae of *Schedius kuvanae* are feeding. ×30. From Howard and Fiske, *U.S. Dept. Agric. Ent. Bull.* 91.

In concluding this brief outline of insect-larvae parasitic on other insects, mention may be made of certain minute Hymenoptera which lay their eggs in the eggs of larger insects, so that their larvae may feed on the contents. *Anastatus bifasciatus* (Fig. 114 *a*), for example, is an egg-parasite of the "Gipsy" moth, and its tiny but stoutly-built larva (Fig. 114 *b*) feeds on the stored food-material of the egg, being adapted for development in eggs before the formation of the lepidopteran embryo has advanced. A little proctotrupid fly (*Schedius kuvanae*), also lays her eggs in the "Gipsy" eggs, but the Schedius larva develops in the unhatched caterpillar rather than in the unabsorbed yolk; in some cases Schedius acts the part of a secondary parasite to Anastatus, as a larva of the latter has been observed within a shell of the "Gipsy's" egg with three Schedius grubs feeding inside its own body (Fig. 114 *d*).

Among these parasites may be mentioned as of especial interest the minute "fairy-flies" (*Mymaridae*) with delicately-fringed wings, some of which dive under water, using their wings as swimming-organs, and lay their eggs in the eggs of dragon-flies within which the tiny larvae feed. The mymarid grub is said to devour the dragon-fly's egg in a few days, and the whole life-history lasts only a fortnight, the imago coming from the pupa enclosed within the host-eggshell, and swimming with strokes of the oar-like wings up to the surface of the water.

The mention of these tiny egg-parasites in connexion with dragon-flies suggests some reference to the large number of insects which in the larval as well as in the adult stages of their life-history live by preying on weaker creatures, which they catch and devour. The dragon-fly's larva (see pp. 44–9) is a typically predaceous insect, that lurks concealed at the bottom of its native pond or stream and stalks smaller larvae; its large size and the nature of its feeding activities differentiate it sharply from a parasitic grub. Yet there are instances in which it is not easy to decide whether a larva ought to be regarded as a parasite or a beast of prey. We may take for example the "digging wasps" (*Pompilidae* and *Sphegidae*)[1] belonging, like the ichneumonoids, to the Hymenoptera, but

[1] J. H. Fabre: "Souvenirs Entomologiques". 1879-1905. G. W. and E. G. Peckham: "On the Instincts and Habits of the Solitary Wasps". Madison, Wisconsin, 1898.

having the female's ovipositor modified into a sting, as is the case also with the wasps, bees and ants. These digging-wasps capture caterpillars, grasshoppers, crickets, spiders, or other creatures—each genus having its own specially appropriate prey—which they sting so as to paralyze, and then bury in the ground, laying eggs on their bodies. The digging-wasp's larvae when hatched proceed to devour the victims, and their manner of feeding is, as a whole, closely like that of the ichneumonoid larvae except that they attack the victim from outside, not from within. Species of *Bembex*, which also belong to this group, furnish, at the time of egg-laying, enough supply of food to serve the larvae during the earlier stages of their growth ; later on the females catch flies wherewith they feed their grubs as a mother-bird her nestlings, till they attain their full growth, and are ready for pupation. Here the insects are evidently hunters, and their larvae cannot be truly described as parasites.

Many insect-larvae, having no such maternal care as is displayed by the Bembecines, are themselves active little beasts of prey. Reference has already been made (p. 109) to the grubs of ground-beetles, which run after insects in the soil, and those of lady-birds (p. 109) which leisurely devour "green-fly" on plants, in much the same way as their parent beetles do. Many other beetle larvae are carnivorous, such as those of the dyticid water-beetles which pierce and suck tadpoles and other aquatic creatures, the "glowworm" which attacks snails and slugs, and those of the rove-beetles (*Staphylinidae*) which hunt plant-feeding grubs in the soil or in timber-galleries. Almost all these predatory larvae are of the well-armoured, long-legged type that shows the least marked difference from the adult form. It is of especial interest to notice this predaceous habit among larvae of other types, which have to make their own way in the world. The adaptation of the maggot for active carnivorous habits is well shown in the larvae of the hover-flies (*Syrphi*)—graceful, little, yellow-banded flies which poise themselves over flowers. Their maggots, like the lady-bird grubs, live on plants and devour "green-fly" which they impale on their mouth-hooks. The Syrphus larva (Fig. 115), has the cuticle tougher than that of an ordinary scavenging or plant-feeding maggot, tuberculate and wrinkled, not pale

and fleshy but mottled with yellow, green, and brown ; its body is compressed from above downwards, and it crawls actively on its flat ventral surface, constantly rearing its tapering front region into the air.

The caterpillar of a moth may be regarded as a larva most typically marked as vegetarian by its structure and habits, yet there are several species of caterpillars that do not hesitate to attack and devour other caterpillars, should the leafy food-supply fail, and some species—such as the noctuid *Calymnia trapezina*—habitually adopt this mode of feeding. They are often described as "cannibals", but this term of reproach should be applied only when caterpillars eat members of their own species, behaviour which appears to be unusual. The

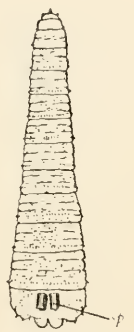



FIG. 115. MAGGOT OF HOVER-FLY (*Syrphus*) (DORSAL VIEW). *sp*, tail spiracles. × 3.

larva of Calymnia and others that display these predaceous habits do not differ in any structural feature from typical leaf-eating caterpillars. The South European moth (*Erastria scitula*) (Fig. 116 *f*), has, however, a caterpillar structurally modified in accordance with a specialized carnivorous habit.[1] It feeds on scale-insects, biting its way through the scale of a large female *Lecanium* and devouring the occupant, after which it adopts the scale as a covering for itself. In keeping with this habit, the caterpillar's body is short and egg-shaped with its tail-region upturned (Fig. 116 *a b c*), so that the hind-most prolegs are attached to the covering scale ; the prolegs

[1] C. V. Riley and L. O. Howard : "An Important Predatory Insect" *Insect Life*, VI. 1894.

of the third and fourth abdominal segments are wanting, those of the fifth and sixth serve with the thoracic legs for locomotion. As the Erastria caterpillar grows it adds fresh scales to its case, which it carries about continually and beneath which it finally spins its cocoon and pupates, after biting a hole through which it can afterwards emerge as a moth.

Our consideration of this caterpillar leads naturally to a fresh aspect of the surroundings of young insects—the varied means by which they secure shelter and protection from enemies. Active, armoured larvae of predaceous habit are protected to a great extent by their firm exoskeleton and their power of rapid motion. In the earlier section of this chapter

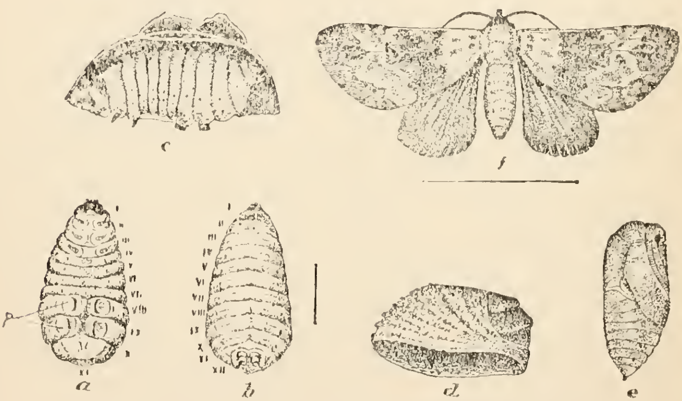


FIG. 116.

*a*, *b*, ventral and dorsal views of the coccid-eating caterpillar of the Moth *Erastria scitula* (*f*), the segments are numbered and the prolegs indicated (*p*); *c*, side view of the caterpillar showing casing of scales in section; *d*, side view of case; *e*, pupa. × (*a*, *b*, *c*) 3; (*d*, *e*, *f*) 2. From Riley (after Rouzaud), "Insect Life", VI.

(pp. 205, 210) examples have been given of many caterpillars and grubs which feed by tunnelling in timber or mining in leaves or becoming enclosed in galls, thus lessening the risks of their lives by their hidden places of living. Many caterpillars, both of moths and saw-flies, which are too large to live between the two skins of a leaf, roll the edges of leaves together and secure them by silken threads; thus they may be said to use their food-supply as a habitation, or to construct edible dwellings for themselves. Well-known examples of this habit are afforded by the caterpillars of the Green Tortrix moth (*Tortrix*

*viridana*), which rolls the terminal part of an oak-leaf transversely into a neat cylinder, and by a saw-fly (*Blennocampa pusilla*), which rolls rose-leaflets closely and longitudinally. The Erastria caterpillar, just mentioned, illustrates the habit of forming a portable case, a more familiar instance of which is afforded by the common clothes-moth (*Tinea*) caterpillars. These spin together the pellets of their own excrement with their silk, and thus build tubular cases which they carry about with them, as they nibble at the woollen fibres of garments or the fur of skins. The tubes formed by midge grubs in ponds and ditches have already been mentioned in this chapter, and among aquatic larvae no group offers more perfect demonstration of the case-building habit than the caddises (Trichoptera, see pp. 122, 141). Caddis-larvae of different families make houses of various objects—fragments of water plants, small stones, snail-shells; and the caddis-house may be portable (*Phryganea*) or fastened to a submerged boulder as are the habitations of the Hydropsychids, beautifully constructed of tiny stones.

These shelters are all made of foreign objects which the larva finds ready to hand, but the objects are fastened together by silk, the creature's own secretion. Many young insects protect themselves entirely with the products of their own bodies. We have seen already (p. 193) the importance to the Simulium grub of its silken labyrinth as an anchorage in the swift streams that it inhabits, and the web-nest spun by the united labour of the small ermine (*Hyponomeuta*) caterpillars (p. 204). Similar silken webs in which the members of a family live as a loosely united community are spun by the caterpillars of the Peacock butterfly (*Vanessa io*) on nettles, and by those of the Lackey moth (*Clisiocampa neustria*) on various trees. The hairy larvae of the Brown-tail moth (*Euproctis chrysorrhaea*) are hatched from the eggs in autumn. They construct a silken web-nest in which they pass the winter, resting and taking no food, but the stimulus of spring sunshine incites them to leave this warm shelter and climb up the shoots and twigs of their food-plant in search of provender after the winter's fast. Many of these web-spinning caterpillars are protected in another way: by an abundant growth of hairs and spines from the cuticle of the body, so that the soft wormlike larva

becomes more or less formidably armoured. Caterpillars of the "tussock" family (*Lymantriidae*), to which belongs the Brown-tail moth, just mentioned, have tufts of long barbed bristles which if incautiously handled, work their way into the skin causing severe irritation and sores. There is much evidence that such hairy and spiny caterpillars are not eaten by insectivorous birds, which devour readily comparatively smooth larvae like those of owl-moths. This hairy clothing is thus a valuable protection and it is probably advantageous also when the species winters in the larval condition, as is the habit of the Brown-tail and of our common Garden Tiger moth (*Arctia caia*). Some of these hairy caterpillars are active in habit and comparatively rapid in movement; the brightly coloured "tussock" larvae of our common Vapourer moth (*Orgyia antiqua*), for example, often migrate from tree to tree across considerable tracts of country, a habit valuable for extending the range of a species whose wingless adult female never feeds, and never moves away from the cocoon whence she emerged. In the earlier stages of their growth, such hairy caterpillars are often carried long distances by the wind. Often hairiness in caterpillars is associated with bright and strongly contrasted colours;[1] the "Vapourer" larva, for example, is adorned with tufts of yellow, black and red, the "Lackey" displays a livery of longitudinal stripes of red and blue, the "Bufftip" is striped black and yellow. There is a considerable mass of evidence, that such conspicuous types of coloration among animals are associated with some noxious or distasteful quality, and insects thus adorned are commonly refused by insectivorous birds. Hence has arisen the general belief that these "warning" colours are advantageous to their possessors, since they serve to advertise inedibility, and are easily recognized by insectivorous animals, which quickly learn by experience to leave conspicuously coloured creatures unmolested. Such "warning" colours are seen also in many caterpillars with comparatively smooth cuticle—such as the "Cinnabar" (*Hypocrita jacobaeae*), with

[1] E. B. Poulton: "The Colours of Animals". London, 1890. "Natural Selection the Cause of Mimetic Resemblance and Common Warning Colours". *Journ. Linn. Soc. Zool.*, XXVI. 1898. G. A. K. Marshall and E. B. Poulton, "Observations and Experiments on the Bionomics of South African Insects". *Trans. Entom. Soc., London.* 1902.

its segmentation vividly marked by transverse bands of black and yellow, found feeding on ragwort in summer ; the " looper " larva of the " Magpie " (*Abraxas grossulariata*), cream-coloured with black and yellow blotches, a familiar object on gooseberry and current bushes in May and June ; or the large caterpillar of the Spurge Hawk-moth (*Deilephila euphorbiae*) with its harlequin particoloured livery of patches and spots In this last-named case inedibility seems associated with the poisonous nature of the food-plant (*Euphorbia*) ; in other cases the larvae secrete a poisonous or noxious repellant which is itself a protection against being eaten, its presence advertised by the brilliant " warning " colour.

A far larger number of caterpillars are, however, coloured on the opposite principle—so as to be hidden through their harmony in tone with their surroundings. As these are greedily eaten by many birds as soon as perceived, it is believed that the concealment that they secure through their likeness to their environment is of value in preserving them from detection and destruction, and the likeness is defined as " protective " resemblance.[1] Most caterpillars which feed on leaves or crawl along twigs are green or brown in colour ; often the green area is interrupted by a pale longitudinal stripe on each side, and in very large caterpillars such as those of hawk-moths (*Smerinthus*), for example, the green area is broken by a series of oblique yellow lines. Such a caterpillar, when feeding, is remarkably inconspicuous. Many of the " looper " caterpillars are wonderfully like the twigs of their food-plants in shape as well as in colour, and this resemblance is accompanied by the habit of stretching the body stiffly out at an angle to the twig grasped by the prolegs on the sixth and tenth abdominal segments. Thus the larva's mode of behaviour co-operates with its appearance to produce the protective resemblance. It has been shown that many of these protectively coloured caterpillars can be induced to change their colours within limits, if they be transferred at a stage sufficiently early from one food-plant to another with leaves and twigs of a different hue ; and these changes are due to a reaction of the subcuticular tissue to the quality of the rays

[1] E. B. Poulton : " The Colour Relations between certain Lepidopterous Larvae, etc., and their Surroundings ". *Trans. Entom. Soc., Lond.* 1892, 1903.

of light reflected from the surroundings. These adaptations shown by larvae during the period of their growth are highly interesting and suggestive to those who think of the problems presented by the relation of living creatures to their surroundings. The habits of the caterpillars, their form and colour, the changes of hue they undergo, are of the nature of responses to their changing environment. But they are living organisms and the power to respond by outward behaviour and internal reaction is part of the creature's innate constitution ; it could not answer harmoniously to its surroundings had it not inherited the power to do so. The inheritance can be traced to the essential substance in the germ-cells whence the creature sprang. These become mature and functional in the adult winged insect which lives under very different conditions from those of the caterpillar. Yet this germ-plasm is so constituted as to provide for the needs of larval life—not only in determining structure and appearance but also in fixing habits of suitable behaviour. Those who believe that the germ-plasm may itself be subject to environmental influence, might remind us that the germ-cells are already undergoing their development within the caterpillar which is identical individually with the pupa and the imago into which it will change.

This reference to characters inherited through the parents suggests a subject which may fitly close this discussion on the environment of insects during their period of growth. Among many animals the family atmosphere, as it may be called, supplies environmental factors of high importance ; common birds and beasts afford examples of the care of parents for offspring, of the comradeship of brothers and sisters. These factors are not strongly evident among insects as a class, yet they are frequently indicated, and in some well-known cases they are developed with characteristic specialization. Comradeship between members of the same family is shown by those caterpillars which live on masses of silken web spun by their collective labour. In the pages of this chapter, repeated mention has been made of the egg-laying habits of various female insects, and it is evident that these habits secure suitable provision for the needs of the young during their time of growth. For comparatively few insect larvae have the power of travelling far in search of food ; the newly-hatched

young must find itself in the midst of an appropriate food supply if it is to survive, and this condition is ensured by the usually certain action of the female in laying eggs in or on the right material. Though comparatively few parent insects, on account largely of the divergence in life-conditions of the larva from the adult, ever see their young, these owe their habitation and food, whatever they may be—the leaf, or the bark-gallery, or the timber-tunnel, or the mass of refuse, or the gall, or the body of a host-animal—to the predictive action of their mother, Maternal care has its part in the environment of all, even if the eggs be dropped with apparent heedlessness on a running stream.

From this common mode of behaviour as regards egg-laying which results in a provision of suitable food and shelter for young insects generally, we may pass to those more interesting cases in which the female sees and tends her young after hatching. Instances of such direct maternal care are found among some insects which display the open type of wing-growth; among those with complete transformation they are more frequent. One of the lowliest exopterygote orders (the Dermaptera) affords in the common earwig (*Forficula*) an example of a mother insect which broods over the eggs until they are hatched and watches the young for some time after hatching. Beneath an upturned stone a female earwig may often be found sitting on her eggs, and later covering the small members of her newly-hatched family with her body. Among the Orthoptera, the female Mole-cricket (*Gryllotalpa*) constructs an underground nest in which she deposits her eggs to the number of three hundred or more, and it is said that she changes the position of these with regard to the surface of the soil in correspondence with changes in the air-temperature due to varying degrees of sunshine. She defends the eggs, as well as the young after hatching, from attack by predaceous ground-beetles, and also from males of her own species, for while the mother's care is exemplary, the father is addicted to cannibalism. Mole-crickets are carnivorous, and the mother catches prey for her young, as well as for herself, until they have undergone their first moult.

The spring and summer aphids which give birth to active young may be seen in numbers on leaves surrounded by their

progeny, but here in the relations of parent and offspring is only proximity without any true association. Some members of this order (the Hemiptera) show, however, quite remarkable parental care. In a species of shield-bug (*Acanthosoma griseum*) not uncommon in these countries, and in several related exotic kinds, the female insect covers the eggs and the newly-hatched young with her body, and behaves as though she regards them with much solicitude. Several observers from the eighteenth century onwards[1] have described how the female *Acanthosoma griseum* at her station on a birch-leaf guards her offspring faithfully, fluttering her wings if touched, " shifting her legs and sloping her shoulders and back, so as to protect the side on which the danger threatens ". As the young shield-bugs grow older they scatter about the twigs of their native tree ; the anxious mother pursues them for awhile, but finally allows them to shift for themselves.

Among the large orders of the Lepidoptera and Diptera no insects are known to display parental care after egg-laying, and such behaviour is very rare among the beetles (Coleoptera). Reference has been made to the bark-beetles (*Scolytidae*), whose females lay their eggs at intervals along the " mother-gallery ", but each grub works along its own lonely tunnel in most cases. Some scolytid beetles of the *Tomicus* group, however, burrow deeply into the wood, where they live in societies, their principal food consisting of certain fungi which have been dignified by the name of " ambrosia ". It has been found that the beetles attend to the culture of these fungi, and they thus provide food for themselves and their larvae.[2] A small European weevil (*Rhynchites betulae*), though it takes no direct care of its larvae, bites curved incisions across birch leaves, which it rolls with wonderful accuracy into narrow, elongate tapering funnels before laying a few eggs in each ; thus the larvae, when hatched, find themselves surrounded by shelter and food, the result of their mother's labour.

Several examples have been given of the egg-laying habits of various Hymenoptera, and it is in this order that the continuance of maternal care after egg-laying is most frequent

[1] G. W. Kirkaldy : " Upon Maternal Solicitude in Rhynchota and other Non-social Insects ". *Entom.*, XXXVI. 1903.

[2] H. G. Hubbard : " The Ambrosia Beetles of North America ". *U.S. Dept. Agric. Entom. Bull.* 7. 1897.

and characteristic. Even among the saw-flies there are remarkable instances of such habits. A Tasmanian species (*Perga Lewisii*) lays her eggs between the two surfaces of an eucalyptus leaf on which she remains until the eggs have been hatched. Then she follows her little caterpillars about as they feed on the foliage, often overshadowing them with her body, " preserving them from the heat of the sun and protecting them from the attacks of parasites and other enemies ".

In the brief survey already given (p. 228) of the habits of the digging wasps, it has been seen how from the storing of nests with prey paralyzed by stinging, alongside which the eggs are laid—perhaps the most striking example among insects of anticipatory parental care—we are led on to such behaviour as is shown by Bembex, whose female not only provides, when laying her eggs, victims for the larvae as yet unhatched, but herself tends and feeds these larvae in the later periods of their growth. Thus is suggested a transition to the care for growing larvae that is displayed by the most highly developed of the Hymenoptera—wasps, bees, and ants. The great majority of the bees have the habit of laying their eggs in chambers alongside a store of food, which is provided beforehand by the mother for the offspring that she will not herself see. The food of bee grubs consists of floral products : honey and pollen, the latter being gathered by the mother from blossoms, while honey is nectar that has undergone digestion within the bee's crop (or "honey-stomach") and has been regurgitated into the comb-chambers. This, and the cultivation of fungi, are perhaps the most specialized modes of vegetarian feeding practised by insects. The care of the mother-bee for her unseen offspring is shown by the elaborate constructional work on the chambers in which the larvae live and feed. Thus, the leaf-cutter bees (*Megachile*) cut, with their mandibles, neat pieces from rose and other leaves, with which they line the underground chambers of their nests. The mason-bees (*Chalicodoma*) of southern Europe make chambers with strong, substantial walls of cement formed of earth and small stones compacted with the insect's saliva ; through this wall the young bee has to bite its way out with its mandibles when the transformation is

complete. These strongly and elaborately-formed nests do not afford complete protection against invasion by " cuckoo "-bees, which lay their eggs within, so that their larvae may absorb the store of food provided by the nest-building bee for her own offspring. Sometimes the inquiline egg is laid earlier than the egg of the nest-maker, or the inquiline grub feeds faster than the rightful inhabitant of the chamber, which is consequently starved. The grub of a species of *Stelis*, which lays her eggs in the chambers of the nest made in hollow bramble-stems by *Osmia* before the eggs of that bee have been laid, finds itself hatching low down in the mass of food on the top of which the Osmia grub is feeding. Both larvae continue to eat until the store provided by the mother Osmia is exhausted and the two meet, when the Stelis larva, which is bigger and stronger than that of Osmia, digs its mandibles into the latter, kills, and devours it.[1] These bees, in which the females are all normal fertile egg-producers, are said to be " solitary " in their habits, for though a number of nests are often made close together there is no development of family life. Similarly many of the wasps have analogous habits, making—as our native species of *Odynerus*, for example,—nest-chambers of masonry, and provisioning them with caterpillars and other insects for the support of their carnivorous larvae.

The communities of the social wasps and bees, as well as those of the ants, arise through the survival of the mother-insect long after the completion of the transformations of her offspring, and through the remarkable modification of the vast majority of these offspring into infertile females or " workers ", the mother-insect being distinguished as the " queen " of the enormous family-state. The workers assist their mother in the construction of the nest and the tendance of the larvae, as among the social wasps and bumble-bees ; or they take over all the activities of the community except egg-laying, as among the honey-bees and ants. In these latter groups the divergence of the worker from the queen is greater than in the former, as illustrated by the elaborate pollen-gathering organs of the worker hive-bee, and by the winglessness of the ant-workers. It is only possible, here, to

[1] K. W. Verhoeff : " Beiträge zur Biologie der Hymenopteren ". *Zool. Jahrb.* (*Syst.*), VI. 1892.

discuss briefly the wide subject of the economy of social insects from the view-point of the early stages in the life-history. Interesting and noteworthy is the fact that the wasp, bee, and ant grubs are tended and fed for the most part by perfect insects which bear to them the relationship of older maiden sisters. In the families of bumble-bees[1] and wasps[2] which last as communities only through one spring and summer in our climate, the larvae from the first-laid eggs are cared for by the queen, the later larvae mostly by the workers. The wasp grubs lie in the hexagonal chambers of the comb, of which successive layers are formed in the nest, the whole structure being composed of paper worked-up out of wood-fragments and spittle by the winged wasps, and receive their food, consisting of insects caught and broken up, the nutritious portions softened and masticated, by the workers. The newly-emerged winged insects are stated to obtain from the mouths of the grubs liquid food, consisting mostly of salivary secretion ; later, when the larva is fully grown, this serves as a silky covering for the mouth of the chamber, within which the pupal stage is passed. The chambers in the underground nests of bumble-bees (*Bombus*) are formed—like the honeycomb (Fig. 117) of the hive-bee (*Apis*)—from wax secreted by abdominal glands. These chambers are used for egg-laying and the rearing of larvae, or for accumulating stores of honey and pollen on which the larvae are fed. Each bumble-bee larva, when fully grown, spins a silken cocoon and pupates, the cocoons being aggregated in clusters. Within the nests, both of wasps and bumble-bees, may be found larvae living as inquilines, the eggs from which they were hatched having been laid by females of related species.

The communities of hive-bees and ants are, as is well known, continuous from year to year, owing to the habit of storing food for the support of the members through the winter. In the hive-bee, the care and feeding of the larvae by the workers reaches a high degree of specialization. The well-known waxen honeycomb, with its approximately regular hexagonal chambers, built by the worker-bees, is largely devoted to the rearing of the grubs, an egg being laid by the queen-bee in

[1] F. W. L. Sladen : " The Humble-Bee ". London, 1912.
[2] C. Janet : " Observations sur les Guêpes ". Paris, 1903.

each chamber of the "brood-comb" (Fig. 117). Unfertilized eggs which will develop into males, are laid in hexagonal chambers larger than the ordinary, while fertilized eggs which produce females, are laid in the ordinary hexagonal chambers if destined to produce workers, and in the large, irregular, rounded "royal" chambers (Fig. 117 *c*), if destined to develop into young queens. The newly-hatched grubs are fed by the workers with honey and pollen which has been swallowed and partly digested; this "royal-jelly" continues to be the food of a queen-larva throughout its life, but a worker-larva receives, in its later stages, ordinary honey and pollen. This differ-

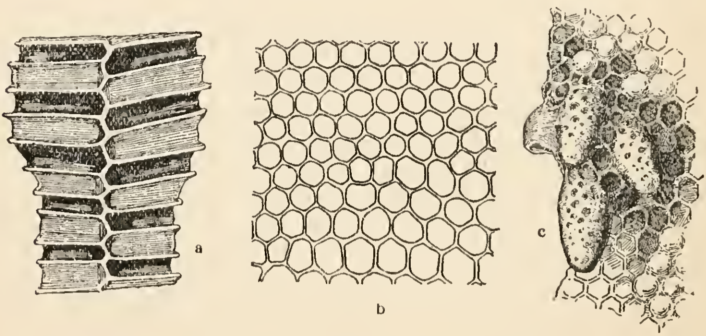


FIG. 117.
*a*, Section of comb of Honey Bee (*Apis mellifica*), showing transition from small ("worker") to large ("drone") chambers; *b*, the same in surface view; *c*, comb with "queen" chambers ⅔ natural size. After Phillips, *U.S. Dept. Agric., Farm. Bull.* 447.

entiation of the two castes of female bees through differential feeding of larvae which are approximately identical in their inherited characters—for a worker larva can be converted into a potential queen by a sufficiently early change of treatment—is one of the clearest examples known of the relative effects of "nature" and "nurture" in bringing about the final result of development in an organism. When the bee grub is fully fed, it spins a delicate cocoon for pupation and the workers seal each chamber with a cap formed of wax and pollen.[1]

In the social communities of ants also, the care and feeding

[1] F. R. Cheshire: "Bees and Bee-Keeping". 2 Vols. London, 1882-5. F. Benton: "The Honey-Bee". *U.S. Dept. Agric. Entom. Bull.* 1. 1895. R. E. Snodgrass: "The Anatomy of the Honey-Bee". *U.S. Dept. Agric. Tech. Bull.* 18. 1910.

of the larvae form an important part of the activities of the worker-insects.[1] In an ants' nest, consisting of galleries and larger spaces excavated in the soil, in timber, or in plant tissues, there are no special chambers of regular shape in which the grubs lie protected. Eggs, larvae, and cocoons are carried about by the worker-ants between their mandibles and deposited in whatever part of the nest seems for the time the most suitable. In many ants' nests the larvae are segregated according to age, and the relation of the adult workers to the brood is much more intimate than among any other insects. The larvae are not only fed but cleaned, and the workers of an American species of *Lachomyrmex*, have been seen to " bring larvae and pupae out on to the large crater of the nest about 9 p.m., and carry them leisurely to and fro, much as human nurses wheel their charges about the city parks in the cool of the evening ". The grubs of most ants differ from the larvae of bees and wasps in the presence of hairs or spines of varying and sometimes complex form often arranged on minute tubercles ; these outgrowths of the cuticle, which are especially evident in the younger larvae, serve to keep them from direct contact with moist earth, to anchor them to the walls of the nest, or to make it easier for the workers to take them up in their jaws without injury. The food provided for the larvae varies immensely among ants of different groups and even of the same kind. Some, like wasp larvae, are carnivorous, others feed on plant-tissues, others on fungi cultivated in the nests, and others again on the secretions of other insects, the honey-dew of aphids, for example. Very many insects which provide such nutritive secretions live as guests in ants' nests, and are carefully tended by the workers as sources of the larval food-supply. In direct reference to the subject of this chapter especial mention may be made of caterpillars of the *Lycaenidae* (Blue Butterflies) which exude, from a gland opening on the dorsal aspect of the eighth abdominal segment, a sweet secretion ; this is used by many ants as food. Ants attend these caterpillars on their food-plants where, as is believed, they protect them from enemies ; some kinds of ants also take the caterpillars into their nests.

[1] W. M. Wheeler : " Ants : their Structure, Development and Behaviour ". New York, 1910.

The care of the worker-ants for the young does not terminate with the final larval stage. Workers often excavate hollow chambers in which the full-fed larvae can conveniently spin their cocoons and pupate. The pupae swathed in their cocoons (the so-called " ants' eggs ") are protected and carried about if necessary by the workers, which afterwards assist the newly-developed adults to emerge from the pupal cuticle and cocoon. Then the prolonged tending of the preparatory instars of the life-history is succeeded by comradeship in the activities of the community among the older and younger adult sister-workers. It may be mentioned that in many ant societies there are several distinct castes of workers differing often in their size, form and functions, as well as aberrant females intermediate to some degree between workers and queens. It must be regarded as doubtful whether, as in the case of the hive-bees, these differences are determined by differences of the food supplied during growth in the larval period.

Ant grubs are thus among the most helpless and quiescent of insect larvae, fed, tended and carried about by their adult sisters. But in a few cases they help in the work of the nest, albeit still in a manner largely passive. Certain genera of tropical African and Eastern ants—*Oecophylla* and *Polyrhachis*, and Brazilian species of *Camponotus* make elaborately-formed nests by fastening the edges of leaves together with silken threads. The adult ants have no silk-producing organs, so they induce the larvae to spin the required material ; while a row of workers hold the edges of the leaves together with their mandibles, other workers bring small larvae which play out silken threads from their mouths as they are moved by their carriers in the appropriate direction, the head-end of each grub pointing forwards and upwards (Fig. 118). As a recent observer[1] has described the process : " There could be no doubt that the ants were actually using their larvae both as spools and shuttles. As several workers toiled close together, they were able to cross and recross the threads and thus produce a rather tenacious tissue ". In the case of some of the species that use their larvae as spinning machines in this remarkable manner, the silk that would normally serve for the

[1] F. Doflein : " Beobachtungen an den Weberameisen ". *Biol. Centralbl* XXV. 1905.

construction of cocoons appears to be all devoted to nest-making, as the pupae have been observed to lie completely unclothed.

This wonderful application to the community work of ants' nests of the silk production characteristic of so many insect larvae, may well conclude our survey of the environment of insects during the preparatory stages of their life-histories. For it illustrates in a striking manner the conclusions to which the facts set forth in this and the preceding chapters tend : the high degree of adaptibility shown by insect larvae in form

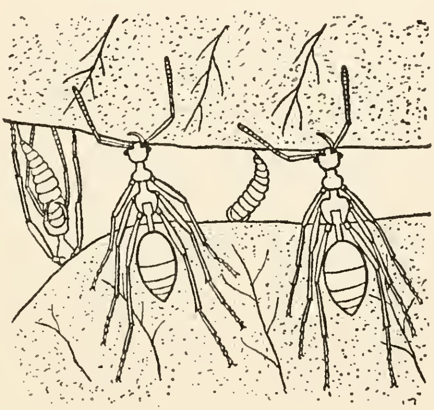


FIG. 118. WORKERS OF THE TROPICAL AFRICAN ANT (*Oecophylla smaragdina*).
Two holding leaf-edges together with their mandibles, and two grasping larvae which are spinning threads so as to fasten the leaves. × 4. After Doflein, *Bio. Centralbl.* XXV.

and behaviour, the divergence in structure and habit from their parents which they exhibit in varying degrees, and the correlation that nevertheless exists between the activities of larva and imago for the working out of the complete life-history. The Oecophylla worker with the spinning grub co-operating, yet passive, held between its jaws, illustrates how, throughout the class of Insects, the larvae, together with the adults, have their share in the weaving of the great intertwined " web of life ".

CHAPTER VIII

# THE PROBLEMS OF TRANSFORMATION

WE have now surveyed some of the more important features connected with the transformation of insects. It remains to consider the meaning of these facts. Not infrequently in the course of the preceding chapters has reference been made to the belief, now universally held by naturalists, that besides the changes undergone by every individual in the course of its life-history, there are changes also in the history of races, and that, to quote Darwin's familiar sentence, " community of descent is the bond which is partially revealed to us by our classifications ". It is also very generally supposed that in the life-history of an animal some suggestions may be found as to the course of evolution in the race to which that creature belongs. A question thus arises as to what light the transformations of insects throw upon the development of the whole class and its various orders through the course of the great periods that mark the progress of life on our earth.

The transformations of insects present a peculiar problem[1] when we compare them with the changes which other animals undergo in the course of their development. Metamorphosis is a feature accompanying growth in many groups of the animal kingdom. We may compare, for example, a bird hatched from the egg, or a puppy or a kitten born, in a form which clearly stamps it as the offspring of its parent, with the infant frog which begins its free life as a fish-like larva, the tadpole, differing from its parents not only in its comparatively undeveloped condition but in such striking outward differences as the absence of limbs and the presence of a tail. Here within

[1] L. C. Miall: " The Transformations of Insects ". *Nature,* LIII. 1895. A. Hyatt and J. M. Arms: " The Meaning of Metamorphosis ". *Nat. Sci.,* VIII. 1896. R. Heymons: " Die verschiedenen Formen der Insectenmetamorphose ", *Ergeb u. Fortschr. Zool.* I. 1909.

the great Vertebrate assemblage the highly-organized, typically terrestrial or aerial classes of Mammals and Birds have no outward metamorphosis, while the partly aquatic and lower-grade class of Amphibia usually pass through a marked transformation. All vertebrates, like animals generally, start their development from a fertilized egg ; the process of growth and change in a bird or a mammal is embryonic, going on within the egg-shell or the mother's womb, while in the life-history of the frog the young creature begins its free life as a comparatively undeveloped larva, which to some extent may be regarded as a precociously-hatched embryo.

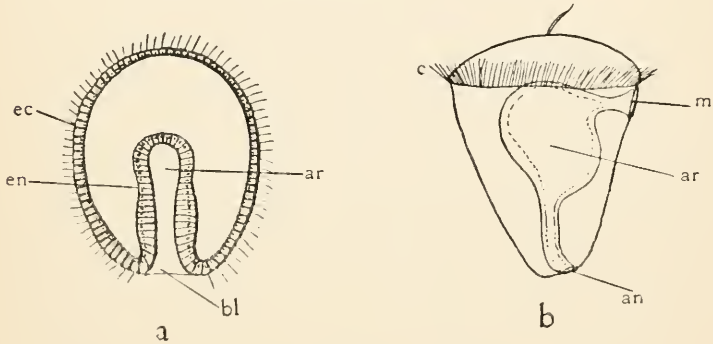



FIG. 119.

*a*, Larva of Starfish in gastrula stage (sectional view) (*ec*, ectoderm with cilia ; *en*, endoderm lining digestive cavity (*ar*) ; *bl*, blastopore) ; *b*, trochophore larva of mollusc (*c*, ring of cilia ; *m*, mouth ; *ar*, digestive tract ; *an*, anus). × about 100.

If we turn to less highly-organized groups of invertebrates, which inhabit the sea, such as the Coelenterata (zoophytes and sea anemones) or the Echinodermata (starfishes and sea-urchins), we find that the developing young usually begins its free life in an extremely early embryonic stage—a minute hollow sac with two cell-layers known as a planula or a gastrula (Fig. 119 *a*)—a stage passed by the frog's tadpole long before the time of hatching. Among more advanced groups, such as the Annelida (segmented worms) and the Mollusca (" shellfish "—oysters, mussels, whelks, etc.), the members of most of the marine families begin free life as a trochophore larva (Fig. 119 *b*), in which there is a definite mouth and gullet leading into the digestive cavity, and a special locomotor organ in the form of a circlet of cilia around the broad head-region.

The trochophore in elaboration of structure is distinctly in advance of the planula or gastrula, but it is in a very early stage of development as compared with the adult into which it has to grow. It is further noteworthy that most annelids and molluscs that live on land—earthworms and snails, for example—are hatched in an advanced stage of development, displaying already the distinctive structural features of their parents ; a minute and delicately-built larva is altogether unfitted for terrestrial surroundings. Also it is well to remember, in making these comparisons as to developmental stages in different groups, that with some marine molluscs, the cuttle-fishes and their allies, the young are not turned out to begin their free life as immature larvae, but are hatched with all the essential features of the adult ; these Cephalopoda have much larger eggs than most Mollusca have, with a rich supply of yolk for the nourishment of the embryo, so that provision is made for its building-up to a high degree of development.

It may now be instructive to turn to various types of growth and transformation that are exhibited by members of various classes of the Arthropoda, the great group of animals in which, as we have seen (pp. 5–6), insects are included. All arthropods produce relatively large eggs with a considerable accumulation of yolk, but they show striking differences in different orders and families as to the degree of change undergone after hatching. If, for example, we take the Crustacea, that class of Arthropoda which are typically aquatic and mostly marine in their manner of life, we find that in the assemblage of orders known as the Entomostraca—comprising the water-fleas, barnacles, and their allies, on the whole low-grade types of Crustacea—the young is hatched as a *nauplius larva,* (Fig. 120 *a*)—a form in some respects highly organized, and yet incompletely grown, having only the three foremost pairs of appendages, the hinder series of segments and their appendages being afterwards developed successively from before backwards through a series of moults. Among the higher Crustacea, on the other hand, the nauplius larva is very rarely found ; either the young is hatched with all its segments and its thoracic appendages, growing the abdominal limbs through a series of moults, with transformation in points of detail, as in the life-

history of the common lobster ; or the newly-hatched creature has its full series of limbs, wanting maybe only the hindmost abdominal pair, which are acquired at the first moult, as is the case with freshwater crayfishes ; or there is a remarkably specialized larva adapted for floating or swimming, whence the crawling adult is developed by a process of rather profound change, as shown in the life-history of sea crayfish and of most crabs (Fig. 120 *b*). Most members of the Arachnida—spiders and scorpions, for example—are hatched or born as miniature

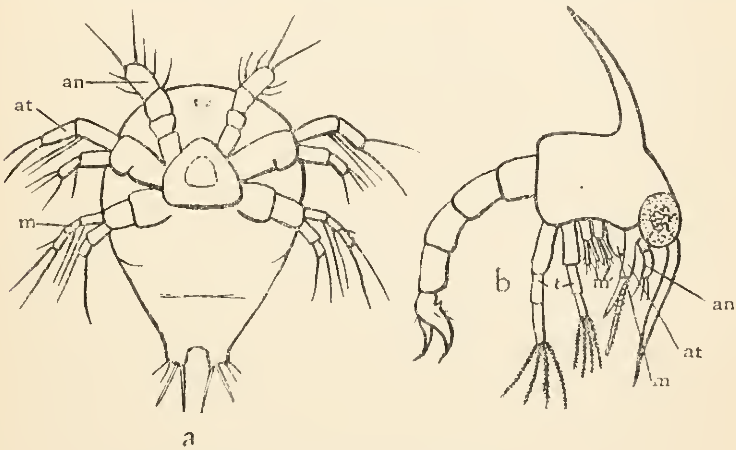



FIG. 120. LARVAE OF CRUSTACEA.

*a*, Nauplius of copepod (ventral view) (*an*, antennule ; *at*, antenna ; *m*, mandible). × 100. *b*, Zooea of crab (side view) (*an*, antennule ; *at*, antenna ; *m*, mandible ; $m^1$, maxillae (two pairs) ; *t*, first and second thoracic limbs ; the abdomen is well developed at this stage, but the hinder thoracic appendages are still rudimentary). × 20.

adults, but newly-hatched mites want the hindmost pair of legs, and in the growth of these little creatures there are often curiously modified stages during which migration or some other crisis in the life-history can be effectually got through. Millipedes are remarkable in being hatched with very few segments and only three pairs of legs, the long series which most of them possess when adult being acquired through a course of moults. The best-known types of centipede (*Lithobius* and its allies), with fifteen pairs of legs when adult, are hatched with only seven pairs, while other families of centipedes leave the egg-shell with their full segmentation already developed.

Now when we compare the various life-histories and differing larval types thus briefly surveyed, a few general principles seem to be apparent. Low-grade animals undergo more profound changes after hatching than high-grade creatures do, jellyfishes and starfishes starting free life, for example, in a condition comparable to the early embryos of vertebrates and arthropods; and within the vertebrate phylum, the lowly, cold-blooded amphibians undergo a transformation unknown among the highly-organized, warm-blooded birds and mammals. The change from marine to terrestrial life appears to be accompanied by the elimination of larval stages from the life-history, as is seen when we compare the newly-hatched whelk with the baby snail, or the trochophore of a sea-annelid with the elongate, well-segmented young earthworm just out of its cocoon. And it may be remarked here that the change from marine to freshwater surroundings also often seems to bring about a suppression or modification of delicate larval forms; the newly-hatched oyster is a ciliated "veliger" larva, while the infant pond-mussel is a "glochidium" already provided with a simple bivalve shell and adapted for attaching itself to some fish on which it may live as a temporary parasite. Animals which produce large fully-yolked eggs rarely undergo marked transformations after hatching, as has been seen in the examples given of cuttlefishes and birds, and as may also be noted in the reptiles (lizards, snakes, tortoises and crocodiles), which though cold-blooded as the frog is, produce large eggs like those of birds, which are indeed so closely akin to them as to have been described by a master in vertebrate anatomy as "transformed and glorified reptiles". The eggs of the non-transforming mammalia are indeed small, but these creatures provide otherwise—by means of the mother's blood—for the rich nourishment of their young before birth.

The transformations of insects seem to offer in many respects startling exceptions to the general rules thus deduced from a comparative study of transformation in other groups of animals. Many insects undergo very striking changes in the course of their growth; yet insects are pre-eminently dwellers on the land and in the air, they produce relatively large eggs with much yolk, and they are the most highly-

organized class among the Arthropoda. It is also abundantly clear that within the class of the insects, the most specialized members undergo the greatest changes ; primitive and comparatively lowly insects like bristle-tails and cockroaches are much like their parents when hatched, but how different it seems with the butterfly's caterpillar, the bee's grub, or the blue-bottle's maggot. We are therefore justified in regarding the transformations of insects as presenting us with a problem of remarkable interest.

In looking for light on this problem it is well to recall the warning (p. 65) that the difference between an insect and its larva may easily be exaggerated. From the brief survey given above of differences in the life-history among various classes of the Arthropoda, it should be realized that no arthropod is hatched in anything approaching the primitive condition that is seen in the gastrula larva of a starfish, the trochophore of an annelid or even the veliger of an oyster. The young nauplius, the simplest type among crustacean larvae, is stamped already as an arthropod because it bears jointed limbs ; it is stamped as a member of the crustacean class because some of those limbs are two-branched. This consideration warns us that transformation among the Arthropoda, though often superficially striking, is far less profound than among several of the great, predominantly marine phyla.

When we pass on to compare insect transformations with the changes undergone by Crustacea and other Arthropods, we notice that while in the latter there is usually necessity for the growth after hatching of many segments and appendages (as in the case of those Crustacea with the nauplius larva, the millipedes, or the centipede Lithobius), in a typical insect larva, such as a ground-beetle grub or a caterpillar, the segmentation and the limbs of the adult are already fully represented. The larva is built on the same general plan as the adult ; it resembles its parent fundamentally, however widely it may differ in details of form. Where, as in such extreme cases as that of the blue-bottle and its maggot, the difference is more striking, more profound, we have seen that the divergence may be interpreted as a case of degradation undergone by the larva, and that the modification of the larva is a specialized—even if a degenerate—condition accompanying

the creature's special mode of life. The peculiar characters of any insect larva are adaptive characters fitting it for its surroundings and its mode of feeding, enabling it to meet the drawbacks and changes of its special life-conditions, which differ in almost all cases from those of the perfect insect. Where—as in the case of the cockroach or grasshopper—the young lives under the same conditions as the adult, it resembles the adult, not only in the great main features of its body-form, but in most points of detail as well. The problem of insect transformation is thus seen to be a problem of the explanation of the origin of many adaptive features in the early life-stages of highly-specialized animals.

This view of the transformation of insects helps us to meet the difficulty mentioned above that the most highly-organized members of the class undergo the most striking changes. In the more primitive orders the newly-hatched insect resembles its parent and throughout the stages of its life-history it lives and feeds in much the same way as its parent does. Such, for example, is the case with a spring-tail or a cockroach. In the more highly-specialized orders the student is struck by marked contrasts, like that between the house-fly and its maggot or between the hive-bee and its grub. All the evidence points to the working out of a process of divergent evolution between the preparatory and the perfect stages; in these most advanced insects the adult has become more and more elaborated, and the larva more and more degraded as compared with the adult. This general conclusion as to the history of insect metamorphosis is now upheld by most students of the subject. We have seen how among the beetles (Coleoptera) a series of larval forms can be traced showing increasing divergence from the adult. Where within this order there are different larval forms in the life-history of the same species (as in the hypermetamorphosis of the oil-beetles), the active armoured larva with relatively long legs precedes the soft, short-legged grub, and where the larval jaws differ least from those of the adult (as in the case of Dascillus and Helodes, p. 104) the presence of distinct maxillulae emphasizes the primitive standing of the type. It thus becomes clear that the maggot represents the greatest departure from the primitive condition among insects, and we understand how with

increasing divergence between imago and larva the resting pupal stage becomes essential so as to give opportunity for the necessary disintegration of larval tissue and the reconstruction of the organs of the winged insect from the imaginal buds.

But if this general conclusion is plain, there remain some points of detail which require elucidation and as to which discussion may be profitable. It may reasonably be asked: (1) If the specialized forms of insect larva have been derived —often through degenerative changes—from a primitive type which differed but little from the adult into which it grew, what clear indications have we as to the nature of this type? (2) If the Endopterygote orders are more highly specialized than the Exopterygota, so that the former may be presumed to have arisen from the latter in the course of the evolution of insect races, how can we imagine the transition from the open to the hidden type of wing-growth to have been brought about? (3) How far do the facts known as to the past history of insects, through a comparative study of the structure of living adult insects and of extinct groups as shown by fossils preserved in the stratified rocks of the earth's crust, support the views on the history of the class of insects which we infer from a study of the life-histories of families now living on the earth's surface?

### THE PRIMITIVE TYPE OF INSECT LARVA

From a comparison of the various larval types presented by the Coleoptera, it has been concluded that the well-armoured, active larva, such as characterizes the carnivorous beetles, the rove-beetles and the dascillids is more primitive than the soft-cuticled grubs of the longhorns or the weevils, with their reduced or vanished legs. This conclusion, though generally admitted by students, has not obtained universal assent. The crawling caterpillar type, recalling the form of a worm or a centipede, has suggested itself to some investigators as indicating the nature of the original insect larva, this view has been revived and ably supported[1] in recent times on the

[1] A. Lameere: "La Raison d'être des Métamorphores chez les Insectes". *Ann. Soc. Entom. Bruxelles*, XLIII. 1899.

ground that the oldest larvae must have lived in concealed situations where burrowing or mining was necessary—a manner of life to which the caterpillar is often admirably adapted. Among the Lepidoptera, whereof the caterpillar is most especially the characteristic larval form, we find that this habit of concealment—mining, burrowing, case-forming—is particularly distinctive of the families of lower grade, such as swift-moths, clothes-moths, the goat-moth family, and the clearwings ; while the caterpillars of the more highly-organized families, like the owl-moths, "loopers", and butterflies, usually

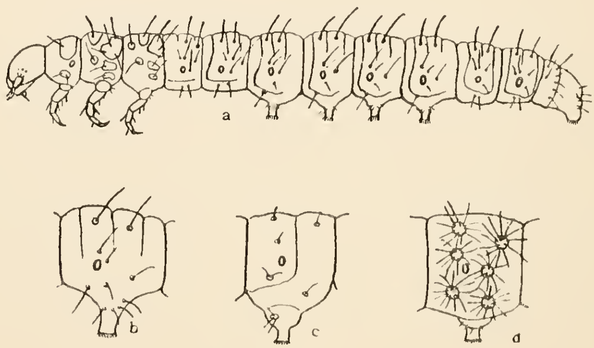



FIG. 121.

*a*, Caterpillar of Swift Moth (*Hepialus*) (side view). × 2. *b*, third abdominal segment of *Hepialus* larva ; *c*, of *Pyralid* larva ; *d*, of "Tiger" (*Arctiid*) larva. × 3. In part after Packard, *Mem. Nat. Acad., Sci.* VII and Dyar, *Ann. N.Y. Acad. Sci.* VIII.

feed openly exposed on leaves. But when the details of the cuticle and armature of a series of lepidopteran caterpillars are studied,[1] it is seen that in their relatively longer legs, more numerous and larger bristle-bearing plates, and well-developed prothoracic and post-abdominal terga, the caterpillars (Fig. 121 *a b*) of these primitive moths approach the active well-armoured beetle larvae, while among the highly-developed Lepidoptera the caterpillar either becomes superficially smooth with a very feebly-developed, bristly armature (*c*), as with most owl-moths and "loopers", or it develops a dense, close covering of protective hairs or spines (*d*) in connexion

[1] H. G. Dyar : "A Classification of Lepidopterous Larvae". *Ann. New York Acad. Sci.*, VIII. 1893. T. A. Chapman : "Some Notes on the Micro-Lepidoptera whose Larvae are external feeders, and chiefly on the early Stages of Eriocephala calthella". *Trans. Entom. Soc.* 1894.

with some special need for protection in its life-conditions (as has been illustrated in a previous discussion on larvae in relation to their surroundings, p. 232) like the conspicuous caterpillars of " eggars ", " tussocks ", and many butterflies.

There is, however, one feature distinctive of caterpillars that may, with much probability, be regarded as a primitive survival : the presence of paired limbs on many of the abdominal segments. There may be seven or eight pairs of these prolegs on the abdomen of a saw-fly caterpillar, and it is well known that five pairs are usual on the larva of a moth or butterfly. These prolegs are clearly adaptive structures, especially suited to the caterpillar's habit of crawling along twigs or the edges of leaves ; but there is no reason to doubt that the embryonic rudiments on the abdominal segments from which they grow, are appendicular in nature, and serial with the thoracic legs like the evanescent limb-rudiments that appear for awhile on certain abdominal segments of some beetle-embryos as well as on those of ants. The truly appendicular nature of prolegs is also strongly supported by the fact that in the moss-eating larvae of the *Micropterygidae* (Fig. 122) these limbs may be jointed like the thoracic legs. And this group of little moths is the most primitive section of all the Lepidoptera, as shown by the undifferentiated wing-nervuration, the presence of mandibles in the imago and in the pupa, and of a lacinia in the maxilla of the adult. A caterpillar-like larva, also with jointed prolegs, is found among the Mecoptera, that small, antique order of which the scorpion-flies (*Panorpidae*) form the principal family.

No coleopteran larva has any trace of abdominal prolegs, but it will be remembered that in those highly interesting insects, the mayflies (Ephemeroptera, p. 93–5), the aquatic larva and nymph has a series of paired abdominal limbs modified into tracheal gills. Mayflies are insects which show a remarkable commingling of primitive with specialized characters in the adult, and their larvae are suggestive of bristle-tails (Thysanura) adapted for life under water ; for they have crustacean mandibles, relatively large and conspicuous maxillulae, long tail-feelers (*cerci*), and a median tail-process, while, as we have just noticed, they possess on the abdominal segments a series of pairs of gills which are modified limbs—structures comparable to the abdominal limbs of a machilid

bristle-tail, but specially adapted to the mayfly-larva's aquatic habit of life. Bristle-tails may with high probability be regarded as the most primitive of insects now living, and the mayfly-larva resembles them not only superficially, but in such important characters as the jaws, limbs, and abdominal appendages. It may therefore be permissible to regard as the most primitive type of insect larva, a form like the mayfly grub before it had become modified for breathing dissolved

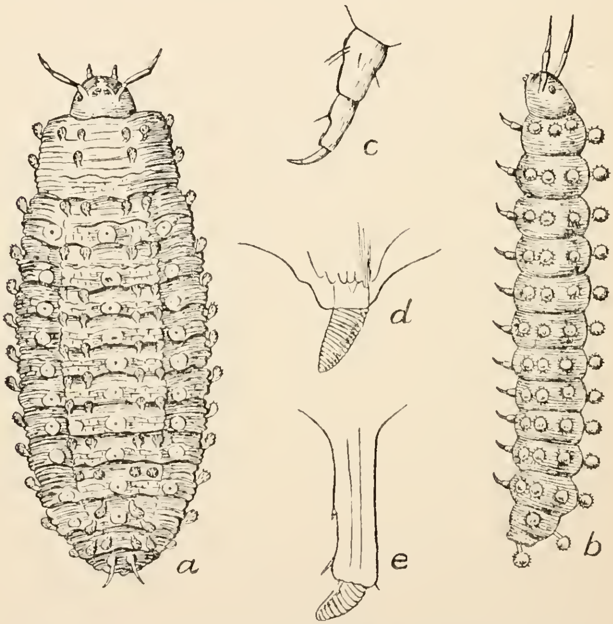



FIG. 122. FIRST-STAGE LARVA OF PRIMITIVE MOTH (*Micropteryx calthella*). *a*, dorsal view; *b*, side view. × 65. *c*, thoracic leg; *d*, abdominal proleg of later larva. × 200. *e*, abdominal proleg of first stage larva. × 600. After Chapman, *Trans. Ent. Soc.* 1894.

air; that is to say with the abdominal appendages not specialized into flattened plates, but slender and probably jointed.

The most primitive type of beetle-larva resembles this in general form, and in the presence of recognizable maxillulae, but has lost all the series of abdominal limbs, while its mandibles are of the normal insectan type like those of its parent beetle, which it may also resemble in its two-clawed foot.

And the caterpillar type, preserving the prolegs—jointed in the antique Micropterygids and Panorpids—can be derived from the same hypothetical primitive larva by an elongation of the body, a restriction of the thickened regions of the cuticle to scattered plates, a shortening of the legs and the disappearance of the cerci. The reduction or disappearance of the legs has evidently occurred independently among the beetles and the Hymenoptera, as well as among the primitive Diptera, and in the last-named order we have already traced the disappearance of the head-capsule, resulting in the evolution of the degraded maggot which exemplifies the extreme type of divergence between an insect larva and its winged parent.

### THE TWO TYPES OF WING-GROWTH

In the preceding section we have compared the larvae of mayflies with those of certain beetles, and with the archaic, wingless bristle-tails. In this comparison there is a suggestion of continuity through the whole class of the Insecta, since mayflies belong to the Exopterygota, beetles to the Endopterygota and bristle-tails to the Apterygota ; and of these three great sub-classes there can be no doubt that the last named is the most primitive, and that the Exopterygota are, both as regards structure and life-history, less highly specialized than the Endopterygota. The insects are the only winged arthropods, and at some period in the history of their development they must have passed from an originally wingless to a winged condition. An analogous transition from creeping to flight takes place in the life-history of the vast majority of insects in the course of their individual lives after hatching. What indications of relationship do we find in the facts of these life-histories ? Did the group of insects that show the open type of wing-growth and those that show the hidden type arise independently from wingless ancestors ? Or were the more specialized Endopterygota elaborated from an originally Exopterygote stock ?

After the demonstration that the same series of main nervures can be traced in all orders of insects, and that these are prefigured by a corresponding set of air-tubes in the

nymphal or pupal wings of members of various orders,[1] it is hard to avoid the conclusion that the whole series of winged insects come from one original stock, that they are a monophyletic group. If this be so, and if the conclusion set forth earlier in this chapter, that in the course of the evolution of insects there has been a divergence between the adult and larval stages, be justified, we are led inevitably to the further conclusion that those orders which practise the hidden method of wing-growth must have arisen from ancestors in which the more primitive open method was the rule. The Endopterygota must have been derived from the Exopterygota.

Here we are confronted with one of the most interesting and difficult problems of insect transformation : how is the transition from the older to the newer mode of wing-growth to be explained ? The divergence between them goes deep and begins at an early stage in the life-history, according as the incipient wing-rudiments grow outwards so as to be covered by the cuticle and to appear after the next moult, or arise as buds to be enclosed by the inpushed pouches so as to remain invisible outwardly until the pupal stage. So great difficulty has been felt in imagining a process of change from one method of growth to the other, that the suggestion has been made of the interpolation of a temporary wingless condition between the two. In previous chapters (notably in Chapter V) many examples have been given of wingless insects that, being clearly related to winged groups, must be presumed to have lost their wings, and it has been seen how among the aphids (p. 73) winged and wingless generations may appear successively in the yearly life-cycle of the same species. The orders of secondarily wingless insects, such as Mallophaga, Anoplura and Aphaniptera, have been grouped together—somewhat unnaturally—in a section called the Anapterygota, and it has been suggested that the ancestors of the endopterygote orders were Anapterygota, that these races having in the course of evolution lost the wings once developed visibly, reacquired them, but with a new method of concealed growth.[2]

The sudden and revolutionary changes necessary in such a transition as this render the explanation incredible, and

[1] J. H. Comstock : " The Wings of Insects ". Ithaca, New York, 1919.
[2] D. Sharp : " Insects " in *Encycl. Brit.*, 10th ed., XXIX. 1902.

some facts in the life-histories of certain Coleoptera suggest a simpler and more natural sequence of events. The larva of *Tenebrio molitor*, familiar as the " mealworm ", has been observed occasionally[1] to bear pairs of outward wing-rudiments on the second and third thoracic segments (Fig. 123 *a*). Also in the life-history of a small ground-beetle (*Lebia scapularis*) it has been recently shown that[2] a " pronymph " stage with short external wing-rudiments (Fig. 123 *b*) precedes the pupal stage (*c*). A similar pre-pupal instar with external wing-rudiments occurs also in some males

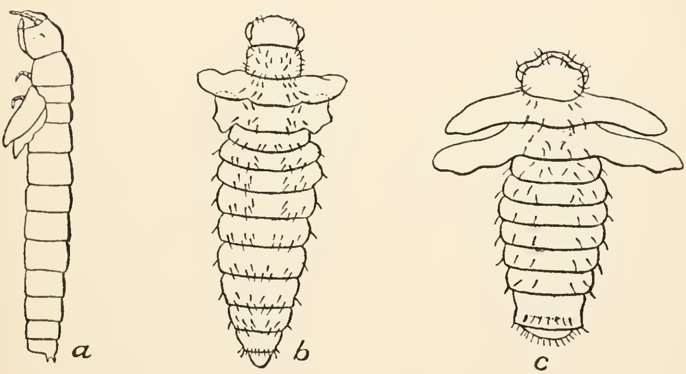



FIG. 123.

*a*, " Mealworm " (larva of beetle, *Tenebrio molitor*) with abnormal external wing-rudiments (side view). × 2. After Heymons, *Ergeb. u Fortschr. Zool.* I. *b*, final larva, and *c*, pupa of ground beetle, *Lebia scapularis* (dorsal view); (*b*, with its small external wing-rudiments is a " pre-pupa "). × 8. After Silvestri, *Redia* II.

of the remarkable parasitic Strepsiptera (p. 118). Such a precocious appearance of wing-rudiments is most unusual among the Endopterygota generally, and in the case of Tenebrio it is abnormal for the species, but it is highly instructive to students of the course of insect transformations, because, if we accept these abnormalities as examples of reversion to an old, ancestral condition, we conclude that among the ancestors of the primitive endopterygote insects wing-rudiments appeared outwardly before the

[1] R. Heymons : " Flügelbildung bei der Larve von Tenebrio molitor ". *Sitzb. d. Gesellsch. naturforsch. Freunde, Berlin*, 1896.

[2] F. Silvestri : " Metamorfosi e Costumi della Lebia scapularis ". *Redia*, II. 1905.

pupal stage in the life-history. And from this it may be reasonably inferred that the stage in which these rudiments appeared became later and later in the history of the more highly-developed orders. The change therefore may be supposed to have begun in an early stage by the small wing-buds sinking into the body so that they could not be covered by the next-formed cuticle, and thus their outward appearance was postponed to successively later stages and finally to the pupal stage. The cases of the beetles just mentioned illustrate the previous condition of their appearance in the pre-pupal stage. And it may be assumed that this difference in the mode of wing-growth was correlated with the increasing divergence between adult and larva to which reference has so often been made in these pages.

In this connexion it is suggestive to notice that among many exopterygote insects, in which the newly-hatched young is a larva differing in aspect from its parent—the *Aleyrodidae* and male *Coccidae* (pp. 86–89), among the Hemiptera, for example—the wing-rudiments grow beneath the cuticle of the resting larva, like those of the pupa in an endopterygote life-history. In these and in other insects, such as the Thysanoptera, the final nymphal form is passive, prefiguring the pupal condition among the higher insects.

The pupa is so distinctive a feature in the transformations of insects of the more specialized orders, that it is of especial interest to find, in the life-histories of simpler types, stages that may be compared with it. Those just mentioned illustrate how, in correlation with special conditions of the life-history, an exopterygote insect may be passive in the stage immediately preceding the adult ; this quiescent, pre-imaginal instar may occur in cases where the young differs but little from the adult (Thysanoptera), or in cases where the young is hatched in a distinctive larval form (*Cicadidae, Aleyrodidae, Coccidae*). On the other hand the mayflies (Ephemeroptera) furnish the unique example of a sub-imago, capable not only of motion but of flight, preceding immediately the adult stage. The comparatively large size of the wings in many endopterygote pupae suggests that the condition now found only in the mayflies may possibly have been general among the primitive insects of early times. And on the other hand it is instructive

to notice how greatly the pupae of the Endopterygota vary in their powers of movement. Where, on account of conditions of life, such as those of the gnat-pupa (p. 197), swimming in the water and using the surface-film for breathing, a considerable degree of mobility is necessary, the pupa may be quite active throughout its term of existence. The caddis-pupa remains quiescent and submerged within the shortened larval house, but in the end it has to bite its way out with its strong mandibles and rise through the water that the fly may emerge into the air. The pupa of a snake-fly (*Raphidia*), of primitive standing among the Neuroptera, has a period of activity before the final moult. And, it has been indicated (p. 140) how among the Lepidoptera, the pupa has a considerable power of motion in the lower-grade families, making its way partly out of the cocoon before the emergence of the moth, while in the higher families it is quiescent except for restricted twitchings of certain abdominal segments. Among such comparatively primitive terrestrial Diptera as the crane-flies (*Tipulidae*) we find that the pupa may work its way upward through the soil, so that the developed fly can emerge into the air, leaving the empty and shrivelled pupa-cuticle protruding from the surface of the earth wherein the larva found shelter and food. In the highly-specialized muscoid Diptera, on the contrary, the pupa remains quiescent within the hardened larval cuticle (or puparium) from which—as well as from the pupal cuticle—the fly, when developed, has to make its escape.

Considering the general indications afforded by these facts it seems clear that the pupa is a specialization from an originally active pre-imaginal stage in the life-history of primitive insects, and that we see manifestations of this activity apparent to some extent in certain primitive families, or in cases where such a mode of behaviour is suitable to the special life-conditions of the pupal period. The quiescence of the pupa is most marked where there is the greatest divergence between imago and larva, and it has already been pointed out that such a resting stage is essential for the reconstruction that must be effected, on account of this divergence, at the end of larval life in preparation for the strikingly different structure and habits of the winged adult.

From these considerations it may be gathered that the metamorphic insects have developed their specialized type of life-history from the simpler and more straightforward course of growth seen among insects of the more primitive groups. It has also been possible to frame suggestions as to the progress of change from the outward to the hidden manner of wing-growth. The question now naturally arises whether this change took place once—in an early stock ancestral to all the Endopterygota ; or whether it may have occurred several times—various orders or groups of orders arising independently from the Exopterygota, perhaps at various periods. In later pages of this chapter evidence of true relationship between the various orders of the higher insects will be brought forward ; but it may be pointed out, how a comparative study of the larval and pupal stages in different orders, supports the view that the Endopterygota form a natural group which had a single and not a multiple origin in the course of the evolution of the insectan class.

The development of the wings and other organs of the imago from ingrowing buds follows a specialized method common in its main features to all the orders of metamorphic insects. This community in the fundamental process of growth indicates community of origin. Then similar types of larvae are found in different orders. The active, armoured, relatively long-legged larva that is characteristic of many beetles is seen also as the early stage in the life-history of megalopteroid Neuroptera, and the larvae of the Planipennia are modifications of the same type, with a special adaptation of the jaws for sucking, analogous to the condition found also in some beetles such as the *Dyticidae.* The legless grub with well-developed head is common to certain beetles (such as the weevils and bark-beetles), to the great majority of the Hymenoptera, and to the more primitive Diptera, while the caterpillar is the characteristic larval form among the Mecoptera, the Lepidoptera and the Hymenopterous saw-flies. These similarities may indeed be explained as convergences due to adaptations to special conditions of life, independently acquired, yet such close likeness could hardly have been reached had there not been a common inheritance of similarly modifiable structures.

The common origin of these orders is indicated also by the close resemblance between the pupae of various groups. The "free" type of pupa is characteristic of all Coleoptera, all Hymenoptera, all Mecoptera, Neuroptera and Trichoptera, and of the most primitive among the Lepidoptera and Diptera. Within these two last-named orders we notice such specializations as the fully obtect pupa of the higher moths and butterflies, and the puparium of the muscoid flies. These specializations within the limits of an order make the general similarity of pupal form throughout the Endopterygota all the more convincing as evidence of true relationship.

## THE HISTORY OF THE INSECT ORDERS

The comparison of larval forms characteristic of various insect groups, has led us to conclude that they may be derived from a primitive type of armoured larva with limbs on most of the abdominal segments in addition to the thoracic legs; such a larva can be compared with some of the primitive wingless insects (Apterygota). We have seen that these Apterygota, as well as the primitive larvae of the mayflies, show in their structure affinity to the Crustacea, and with differences of opinion on points of detail, there has been during recent years an increasing tendency[1] to regard Insects and Crustacea as truly related. The growth of insect-wings has been a recurring theme in this book; our knowledge as to the origin of wings in the whole insectan class is scanty and uncertain, because insects as a class are not abundant as fossils,[2] and the earliest insects, whose remains are preserved to us entombed in European and American rocks of Upper Carboni-

[1] E. R. Lankester: "The Structure and Classification of the Arthropoda". *Quart. Journ. Microsc. Sci.*, XLVII. 1904. G. H. Carpenter: "On the Relationship between the Classes of the Arthropoda". *Proc. R. Irish Acad.*, XXIV. 1903. "Notes on the Segmentation and Phylogeny of the Arthropoda". *Quart Journ. Micr. Sci.*, XLIX. 1905.

[2] For readers unfamiliar with geological nomenclature, the following list of names given to the various divisions of stratified rocks, as distinguished by means of the fossils that they contain, may be useful. The systems are

ferous age, had well-developed wings which served already as efficient organs of flight.[1] But we know that wings arise in exopterygote insects as outgrowths from the second and third thoracic segments, and in *Stenodictya* (Fig. 124), a fossil insect from the Carboniferous beds of Commentry, France, there are paired, flattened outgrowths on the prothorax and

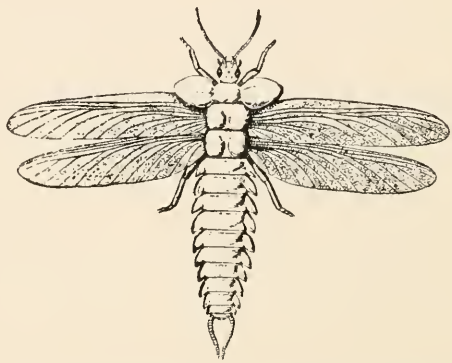


FIG 124. A PALAEOZOIC INSECT (*Stenodictya lobata*). from the Carboniferous of Commentry, France. $\frac{2}{5}$ natural size. After Handlirsch, 1 *Congr. Int. Entom.* 1910.

on eight of the abdominal segments, which, from the aspect and markings, seem to be comparable to wing-rudiments. It has, therefore, been suggested that the ancestors of all winged insects had a series of such paired outgrowths all along the

arranged in " descending " order, the newer formations above, the older below, as they occur generally in nature :—

| | |
|---|---|
| TERTIARY OR CAINOZOIC. | Pleistocene.<br>Pliocene.<br>Miocene.<br>Oligocene.<br>Eocene. |
| SECONDARY OR MESOZOIC. | Cretaceous.<br>Jurassic.<br>Trias. |
| PRIMARY OR PALAEOZOIC. | Permian.<br>Carboniferous.<br>Devonian.<br>Silurian.<br>Cambrian. |

[1] A. Handlirsch : " Die fossilen Insekten und die Phylogenie der rezenten Formen ". Leipzig, 1906-8. J. H. Comstock : " The Wings of Insects ". Ithaca, New York, 1918.

body which may originally have been of service as parachutes, and of these the two pairs on the mesothorax and metathorax became greatly enlarged and hinged on to their segments so as to confer on their possessors the power of flight. It is of interest to note that the larvae of some termites (*Coptotermes*) have on the prothorax elongate wing-like organs[2], which disappear in later stages.

There can, however, be no doubt that the earliest insects known to us developed their wings outwardly, because nymphs with visible wing-rudiments have been recognized among them. Most of them are grouped in an order called the Palaeodictyoptera, characterized by a close similarity between the fore- and hindwings, and by a type of nervuration whence that of the Isoptera, the Plecoptera, and the Orthoptera might alike be derived. Many of the Palaeodictyoptera had the general aspect of cockroaches, and forms of Carboniferous age—such as the North American *Spaniodera*—appearing to lead definitely towards the orthopteroid type of wing-differentiation, have been relegated to an order Protorthoptera. Thus the oldest insects, of which remains have been preserved for study, are seen to have been for the most part Exopterygota allied to those orders now living in which there is least difference in form between the adult and the young.

Contemporary with these ancient insects lived some which may be regarded as representing an early type of mayfly—the order Protoephemerida—of which *Platephemera*, from the St. John's shales (Upper Carboniferous) of New Brunswick, is the best known. In these primaeval mayflies there was a close similarity between the fore- and the hindwings, and among intermediate forms whose remains are preserved in rocks of Jurassic age, the hindwings are less reduced than those of modern mayflies. As to life-history it must remain questionable if the mayfly-like insects of the Carboniferous underwent transformations similar to those of recent mayflies. But a Permian mayfly-nymph with paired gill-appendages on nine abdominal segments has been preserved for our study in Russian rocks, so the characteristic transformation had become

[2] E. Bugnion and C. Ferrière: "L'Imago du Coptotermes flavus. Larvæ portant des Rudiments, d'Ailes Prothoraciques". *Mém. Soc. Zool. France*, XXIV. 1911.

by then established. It will be remembered (p. 181) how the mayfly larva and imago both preserve characters, indicating crustacean affinities, more primitive than can be found in any other group of winged insects, and suggesting that for the ancestors of the order we must probably look near to the base of the exopterygote stock. And this is exactly the conclusion suggested also by the scanty sample of related fossil insects, for the precursors of the mayflies were contemporary and collateral with the ancestors of orthopteroid insects.

The same conclusion may be stated with some confidence as regards the dragon-flies. From the coal measures of Commentry, France, a large number of palaeozoic insects have been described,[1] among them the gigantic *Meganeura*, with a wingspread of more than two feet, and the aspect of a modern dragon-fly, but with the wing-nervuration less remarkably specialized, the radial sector not invading the area of the median nervures as it does in most recent Odonata. These ancient Protodonata, as they are called, persisted into the Permian (the newest sub-division of the Palaeozoic or Primary life-epoch), to be succeeded in Mesozoic or Secondary times by typical dragon-flies whose remains are preserved in rocks of Liassic and Jurassic age (the famous "lithographic stone" of Solenhofen being especially rich in such fossils), referable not only to the same order (Odonata) as our living dragon-flies, but in most cases to existing sub-families. As to the life-histories of the Carboniferous Protodonata we have no certain knowledge; it has been suggested that their early instars lived in damp earth rather than in water. But the Mesozoic dragon-flies resemble recent genera so closely that we can have no doubt as to the similarity of their life-histories; and from the Oeningen beds in southern Germany, of Cainozoic or Tertiary (Miocene) age, a large number of fossil libelluline larvae have been disinterred, of which it is stated that "some had the labial mask projecting, as if in the act of striking their prey". The dragon-fly stock had thus already made considerable progress towards its high development in Carboniferous times; the differentiation between imago and larva

[1] C. Brongniart: "Récherches pour servir à l'Histoire des Insectes Fossiles des Temps Primaires". St. Étienne, 1893.

must have already at that period become marked, and the origin of the order must be sought, like that of the mayfly stock, among those most primitive exopterygote insects of Devonian or perhaps even Silurian age, of which no fossil remains have yet been discovered.

With regard to the third order of exopterygote insects with aquatic gill-breathing larvæ—the Plecoptera or stone-flies—we have little direct evidence from fossils, but a few specimens of Jurassic age can be referred to the living family *Nemouridae*, and nymphs as well as adults are represented among these remains. In the stone-flies there is a much closer likeness between imago and larva than in either the mayflies or dragonflies, and they may probably be regarded as a direct offshoot from the Palaeodictyoptera.

In all these three orders of exopterygote insects with aquatic larvae, shown by the evidence of fossils to be not very closely akin to each other, we find that the larvae breathe dissolved air by means of gills diversely specialized in each order, the gills of the stone-fly larvae being branching tufts on the thorax, of the mayfly grubs modified and flattened serial abdominal appendages, of the dragon-fly grubs modified terminal abdominal appendages or outgrowths from the wall of the hind-gut. These divergences prove conclusively that the aquatic habit of the larvae has been independently acquired in the three orders, while the combination of the gills with air-tubes—a type of breathing organs almost exclusively associated with aerial or terrestrial life—shows that it is during the preparatory stages of the life-history that these insects are in foreign environment. The air is their native element, and the wonderful aquatic larval adaptations are secondary.

The remaining large and important exopterygote order, the Hemiptera, stands apart to a great degree, at the present day from the other orders. Its two sub-orders, the Heteroptera and the Homoptera, are sharply distinguished from each other not only in structure but in life-history, for while young Heteroptera resemble their parents in general body-form, most families of Homoptera afford examples of change during the period of growth. It is of especial interest, therefore, to find in a famous fossil (*Eugereon*) from the Lower Permian of Oldenburg, the characteristic piercing and sucking jaws of

the Hemiptera, associated with the primitive palaeodictyopteroid type of wing ; even if *Eugereon* cannot be regarded as on the direct line of ancestry of living Hemiptera, it suggests clearly that this order had a common origin with the exopterygote biting insects. In Russian Upper Permian rocks there have been found fossil remains of an insect (*Prosbole*), with forewings in which the basal and terminal regions are imperfectly differentiated as corium and membrane, so that it may be referred to a sub-order (Palaeohemiptera) intermediate in character between Heteroptera and Homoptera. Fossils from the same geological horizon, both in Russia (*Scytinoptera*) and in New South Wales (*Permoscarta*) may be safely regarded as ancestral Homoptera,[1] and in Triassic times there were already differentiated the main family groups of Homoptera as we know them to-day. At the same period a primitive family (*Dunstantiidae*) of the Heteroptera was also established, while in the subsequent Jurassic period specialized families of Heteroptera—both terrestrial (*Reduviidae* and *Lygaeidae*) and aquatic (*Gerridae* and *Belostomidae*)—are represented by well-preserved fossils. The divergence between Heteroptera and Homoptera as regards life-history has already been recalled ; it is interesting to note that one of the most dominant of modern homopterous families, the *Aphididae*, retains a type of life-history like that of the Heteroptera with little or no transformation. This family belongs to the same section of the sub-order as those families—the *Aleryrodidae* and *Coccidae*—which display the most remarkable transformations of any exopterygote insects (pp. 86–90). It is probable that this section of the Homoptera diverged from the rest of the sub-order in Permian times, though we have no direct fossil evidence of this.

Turning now to the Endopterygota or insects that undergo complete transformation with a pupal stage, we have already (pp. 260–1) adduced evidence from the striking correspondences in the larvae and pupae of various orders that this sub-class forms a natural group with a common origin from the primitive Exopterygota. In correlation with this view, it

[1] R. J. Tillyard : " Mesozoic Insects of Queensland : " Hemiptera Heteroptera ". *Proc. Linn. Soc. N.S. Wales*, XLIII, 1918 ; and " Hemiptera Homoptera ", *Id.* XLIV. 1919.

is satisfactory to notice how several recent students,[1] from comparative studies of wing-nervuration and other imaginal structural features, have agreed in regarding all the metamorphic insects as derived from a common parent stock.

All the scanty available evidence from fossils confirms the belief founded on the study of the structure and life-history of recent insects, that the Endopterygota appeared later than the Exopterygota in the history of life on our globe. While examples of the latter are comparatively abundant in Carboniferous rocks, the known metamorphic insects of the Palaeozoic era are represented for certain only by two genera (*Permochorista* and *Belmontia*) both from the Upper Permian coal-measures of Belmont, New South Wales.[2] Of these the former is referable to the Mecoptera (scorpion-flies) and does not differ materially in wing-nervuration from members of that order still living in Australia. The latter appears to have possessed a type of wing-nervuration probably modified from that of the Carboniferous Palaeodictyoptera and from which the nervuration of both the Trichoptera and the Lepidoptera might readily have been derived, while the special order (Paramecoptera) to which it is referred by its discoverer stands close to the root of the Neuroptera. In these ancient insects, therefore, we have an indication of the origin of the metamorphic insects generally, and from a consideration of the larvae of existing scorpion-flies (Mecoptera) and alder-flies (Megalopteroid Neuroptera) we may reasonably conclude that the larvae of the unknown common ancestors of these two groups were polypod like the caterpillars of the former and well-armoured with long thoracic legs like the larvae of the latter—exactly the type of larva which our comparative studies, summarized in previous pages, lead us to regard as primitive.

From these Permian insects a succession—incomplete, indeed, but suggestive—leads on to the insectan orders and families of the modern world. *Triadosialis*, from the Lower

[1] C. Börner : " Zur Systematik der Hexapoden ". *Zoolog. Anz.*, XXVII. 1904. G. H. Carpenter : " Hexapoda ", in *Encycl. Brit.* (11th ed.), Vol. XIII. 1906.

[2] R. J. Tillyard : " Permian and Triassic Insects from New South Wales ". *Proc. Linn. Soc. N.S. Wales*, XLII. 1917. " A Fossil Insect Wing belonging to the new order Paramecoptera ". *Id.* XLIV 1919.

Trias of Germany, is definitely referable to the megalopteroid division (alder-fly and snake-fly group) of the Neuroptera; and *Archepsychops* and *Protopsychopsis*, from the Upper Trias of Queensland, belong to the planipennian (lacewing and ant-lion division) of the same order. These divisions are both represented by fossils preserved in rocks of later age—Jurassic, Cretaceous, Tertiary—and are probably less prominent in the insect fauna of to-day than they were in that of the Mesozoic or Secondary life-era. The Mecoptera (scorpion-flies), also represented by fossils of Triassic age, pass on with comparatively slight modification to our own day, in which, however, the few existing families are clearly the survivors of an assemblage more dominant in Mesozoic times. These two orders, the Mecoptera and Neuroptera, must, therefore, be regarded as relatively ancient and primitive.

The Paramecoptera (*Belmontia* of the Australian Permian) are not only recognizable as nearly collateral with the Neuroptera; in their nervuration they show a condition from which both that of the Trichoptera (caddis-flies) and that of the Lepidoptera (moths and butterflies) can be directly derived, so that they have been reasonably claimed as ancestral to those two orders, whose rather close relationship to each other has been recognized by all modern students of insects. The oldest known caddis-flies are the *Necrotauliidae* from the European Lias (Lower Jurassic), to which the existing *Rhyacophilidae* are nearly akin. The evidence of fossils shows, therefore, that the Trichoptera are later in origin than the primitive neuropteroid insects, and it has been pointed out (pp. 122–3) how the caddis larva is modified, in accordance with its water-dwelling, case-building habit from the campodeiform type. The Lepidoptera, with their highly-specialized sucking mouth-parts, are a more advanced order than the Trichoptera, and their oldest-known fossil representatives are an Upper Jurassic family, the *Palaeontinidae*, preserved in English and German rocks. These appear to be collateral with our two existing sub-orders—the Homoneura and Heteroneura (see pp. 184–5)—but ancestral to neither; probably the earliest Lepidoptera (Homoneura) were Liassic in age, and their fossil remains are still unknown. Comparing the early stages of Trichoptera and Lepidoptera, it is remarkable

to find that in the latter order, much more highly specialized in the structure of the imago, the abdominal larval legs, lost in caddis-grubs, are partly preserved in a highly modified form. Also the full set of wing-tracheae are preserved in the lepidopteran pupa, while in the trichopteran there are only two of the original series. It is safe to infer that the pupal wing of the Paramecoptera had a full set of tracheae. Lepidoptera are very poorly represented among fossil insects, as might be expected from their delicate structure and terrestrial habit; it is not until rocks of Tertiary age are reached—notably those at Florissant, Colorado, and Oeningen, Baden—that fossil butterflies and moths are found in any great variety, and these are all referable to existing families.

The Diptera are, as we have seen, the most highly specialized of all insects as regards structure and life-history. But the wing-nervuration of the more generalized Diptera shows points of correspondence with that of scorpion-flies, and an extinct family the *Mesopsychidae*, from the Upper Trias of Queensland, serves to indicate a transition from the primitive Permian Mecoptera to the earliest-known true Diptera of the European Lias. These are referable to the Orthorrhapha whose larvae are grubs with definite head, but without typical limbs; the presence of prolegs in some of them is probably merely analogous to the condition in the mecopterous caterpillar, though the dipteran grub is clearly derivable from such a caterpillar type. The earliest Cyclorrhapha known are of Tertiary age; these are characterized by the maggot as the larval stage, in which degradation is carried to its extreme degree, and their late appearance in geological time confirms the conclusion as to their high specialization which is reached by a study of their form and life-history.

There remain for consideration two large and important orders of metamorphic insects, the Coleoptera (beetles) and the Hymenoptera, as to whose origin there is little or no direct evidence from fossils. The beetles must be an ancient order, despite the specialization of their forewings, because elytra and other remains have been found in the Triassic rocks of Switzerland and also of Queensland (Australia), and some of these are referable to the more specialized families such as the leaf-beetles (*Chrysomelidae*) and the weevils

(*Curculionidae*). In Jurassic rocks the remains of Coleoptera are fairly abundant, the English Purbeck having yielded bark-beetles (*Scolytidae*), while from Tertiary deposits such as those of Florissant, Colorado and the Prussian Amber (Oligocene) and the Miocene marls of Oeningen, a large number of fossils referable to living genera have been described, including some 400 species of weevils. The mandibulate jaws of adult beetles and the primitive, campodeiform type of larva that characterizes many of their families (pp. 99–106) suggest relationship to the Megaloptera, and their ancestral stock must be sought in Palaeozoic times—probably at the latest from the older Permian—before the mecopteroid and megalopteroid branches had diverged from the primaeval Endopterygota.

The Hymenoptera with their combination of biting mandibles, suctorial labium, wings with reduced and specialized nervuration, foremost abdominal segment annexed by the thorax and numerous kidney-tubes, stand apart from all other endopterygote insects, and the earliest known fossils, very few in number from the Jurassic beds of Germany and Spain are referable to both the existing sub-orders, Apocrita and Symphyta. In deposits of Tertiary age Hymenoptera became more numerous, and the most specialized of recent families—such as bees and ants—were living in Oligocene and Miocene times. The caterpillar larvae of the saw-flies are analogous to those of the moths and butterflies; while the likenesses between them may be due rather to parallel evolution than to near relationship, it is suggestive that the arrangement of bristle-bearing tubercles on the segments of primitive moth-caterpillars can be derived by reduction from that which characterizes saw-fly caterpillars.[1] The Hymenoptera must have arisen far down the endopterygote stem; possibly having a common origin with beetles, but more probably as an early offshoot from the primaeval Mecoptera, rapidly becoming highly specialized, not only in the structure of the imago of the higher families combined with the degeneration of their larvae into small-headed, legless grubs, but also in the elaboration of their modes of behaviour leading on to

[1] H. G. Dyar: "A Classification of Lepidopterous Larvae". *Ann. New York Acad. Sci.*, VIII. 1893.

those highly-organized family and social life-relations which fascinate students of their habits in these latter days.

In this brief and imperfect discussion of the problems presented by the transformations of insects, it has been seen how details of the varying life-histories of different types—grasshopper, dragon-fly, beetle, butterfly, bee, blue-bottle—throw light on the development of the class as a whole through the ages of geological time As one traces the life-cycle of an individual insect, lasting perhaps for a few weeks only, or at most for a few years, it is inspiring to think of the changing forms and conditions which are indicated in the countless thousands of generations of the creature's ancestry, reaching back to the far-off period of the Coal-Measures and beyond. The changes undergone by the humblest insect may serve to introduce the observer to the great mysteries of life. In the interpretation of these long, racial life-histories there is considerable uncertainty in many points of detail and in some features of importance. It is right, therefore, that the student approach these questions with humility, because his knowledge is but " in part ", as well as with teachable spirit and with open mind. It is necessary also that the hope of attaining fuller knowledge should be a constant incentive to research, and such hope is possible only to those who have faith that there is an orderly scheme of things into which, with growing comprehension, the humble and the teachable may enter. As we turn back to the observation of the myriad insects of our countryside, from which our discussions started, we hear again, in their cheerful noise, some notes in the great call of Nature to the earnest student :

" Come, wander with me," she said,
" Into regions yet untrod,
And read what is still unread
In the manuscripts of God."

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